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Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

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New Publication Policy for NRC Research Journals

In this issue of the *Canadian Journal of Fisheries and Aquatic Sciences*, we are publishing the new publication policy of Research Journals, National Research Council of Canada, which has recently been approved by the Executive Committee of Council. This publication policy was developed after recommendation by the Advisory Board on Scientific and Engineering Communications (ABSEC) and in consultation with the Editors of the 14 journals published by Research Journals.

In the past couple of years, Research Journals has completely reviewed its publishing policies and procedures. This document formalizes the editorial and production policies, giving all those involved in the editorial and publication process a set of guidelines within which to operate. Briefly, this document describes the responsibilities of authors, editors, the Editor-in-Chief, reviewers, and the publisher and includes publishing policy on copyright, language of publication, the use of Système international d'unités, and advertising. It is anticipated that this publication policy will help us to protect the integrity of the publishing process of the NRC Research Journals program.

Nouvelle politique de publication des Revues scientifiques du CNRC

Vous trouverez, dans le présent numéro de le *Journal canadien des sciences halieutiques et aquatiques*, le libellé de la nouvelle politique de publication des Revues scientifiques du Conseil national de recherches du Canada, qu'a récemment approuvé le Comité exécutif du Conseil. La nouvelle politique de publication a été élaborée suite à une recommandation de la Commission consultative des communications scientifiques et techniques (CCCST), en consultation avec les directeurs des 14 revues scientifiques publiées par le CNRC.

Au cours des deux dernières années, le programme des Revues scientifiques a complètement révisé ses politiques et procédures de publication. La nouvelle politique vise à officialiser les politiques éditoriales et de production et à offrir des lignes directrices communes à toutes les personnes participant au processus éditorial et de production des Revues. Le document en question décrit les responsabilités des auteurs, des directeurs scientifiques, du directeur général, des examinateurs ainsi que de l'éditeur et couvre les politiques relatives aux droits d'auteur, à la langue de rédaction, à l'usage du Système international d'unités et à la publicité. Nous misons sur cette politique de publication pour assurer et protéger l'intégrité du processus de publication du programme des Revues scientifiques du CNRC.

Bruce Dancik
Editor-in-Chief, Research Journals/ Le directeur général, Revues scientifiques

Secretory Synthesis of Active Recombinant Fish Growth Hormone by Insect Cells Using a Baculovirus Vector

H.J. Tsai[1] and H.M. Chen

Institute of Fisheries Sciences, National Taiwan University, Taipei, Taiwan 106

and C.F. Lo

Department of Zoology, National Taiwan University, Taipei, Taiwan 106

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A growth hormone cDNA of yellowfin porgy (*Acanthopagrus latus*) was inserted into baculovirus vectors, pAcT7, under the control of the polyhedrin promoter. A 22-kilodalton (kDa) protein, similar to that of native growth hormone, was detected in the supernatant of insect cells infected with the recombinant virus at the level of 2–8% of total proteins. This protein was immunoprecipitated with rabbit polyclonal antibodies raised against native chum salmon (*Oncorhynchus keta*) growth hormone. Furthermore, a radiolabeled protein band of 22 kDa was also seen in the recombinant-virus-infected cell culture supernatant after labeling with [^{35}S]methionine. Injection of individual tilapia with 0.1 μg of crude supernatant protein containing recombinant growth hormone once a week resulted in significant increases ($p < 0.01$) in weight (54%), weight gain (260%), length (21%), and feed efficiency rate (210%) relative to a similarly treated control group and an untreated control group at week 5 onwards.

L'ADNc encodant l'hormone de croissance chez *Acanthopagrus latus* a été introduit dans des vecteurs de baculovirus, pAcT7, sous le contrôle du gène promoteur de la polyédrine. Une protéine de 22 kilo-dalton (kDa), semblable à celle de l'hormone de croissance native, décelée dans le surnageant de cellules d'insecte infectées par le virus recombinant, représentait de 2 à 8 % des protéines totales. On a effectué une immunoprécipitation de cette protéine en présence d'anticorps polyclonaux de lapin dirigés contre l'hormone de croissance native du saumon kéta. De plus, une bande de protéine de 22 kDa radiomarquée a également été observée dans le surnageant de la culture cellulaire infectée par le virus recombinant après marquage à la [^{35}S]méthionine. L'injection à chacun des tilapia de 0,1 μg de protéine brute du surnageant contenant l'hormone de croissance recombinante, une fois par semaine, a entraîné des augmentations importantes ($p < 0,01$) du poids (54 %), du gain de poids (260 %), de la longueur (21 %) et de l'indice d'efficacité alimentaire (210 %) par rapport à un groupe témoin traité de la même façon et un groupe témoin non traité à partir de la cinquième semaine.

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Growth hormone (GH) is one of the polypeptide hormones produced in the proximal pars distalis cells of the pituitary gland to regulate the growth and metabolism of vertebrates. It has been demonstrated that GH can enhance the appetite, food conversion efficiency, and growth rate of fish (Donaldson et al. 1979). The GH cDNA of chum salmon (*Oncorhynchus keta*) has been cloned and its expressed product recombinant GH (rGH) shown to accelerate the growth rate of fish (Sekine et al. 1985). This finding makes GH cDNAs potentially useful for the production of rGH in microorganisms for research and other applications. Therefore, GH cDNAs have been studied extensively in many species of fish (Sekine et al. 1985; Agellon and Chen 1986; Gonzales-Villasenor et al. 1988; Momota et al. 1988; Saito et al. 1988; Sato et al. 1988b; Watahiki et al. 1988; Hew et al. 1989; Rentier-Delrue et al. 1989; Funkenstein et al. 1991; Tsai et al. 1993a). A number of studies on GH cDNAs focused on expression in either *Escherichia coli* (Sekine et al. 1985; Agellon and Chen 1986; Saito et al. 1988; Sato et al. 1988a, 1989; Rentier-Delrue et al. 1989; Tsai and Tseng 1992) or *Saccharomyces cerevisiae* (Hayami et al. 1989; Tsai et al. 1993b). However, both the *E. coli* and yeast expression systems have disadvantages. In *E. coli*, the highly expressed products are accumulated within inclusion bodies in a denatured and unmodified form (Goeddel 1990). It is a complicated and expensive process to renature the rGH before it is ready to use. In yeast, the construct plasmids in the yeast transformant are generally unstable (Rose and Broach 1990).

The baculovirus genome offers an alternative expression system for eucaryotic genes. The gene of interest is ligated into a vector under the control of the polyhedrin promoter, flanked by viral sequences. Recombinant baculoviruses result from the insertion of the construct gene into the viral genome by homologous recombination in vivo (Summers and Smith 1987). Many recombinant gene products produced by this system have been shown to undergo proper secretion, folding, and posttranslational processing and to maintain biological activity (Luckow and Summers 1988; Miller 1988).

[1]Author to whom reprint requests should be addressed.

GH cDNA of the yellowfin porgy (yp) (*Acanthopagrus latus*), a maricultured fish, has been cloned and sequenced (Tsai et al. 1993a). It consists of 915 base pairs (bp) and encodes a pre-GH of 204 amino acids (aa) including a signal peptide of 17 aa. The 5′- and 3′- untranslated regions are 52 and 231 nucleotides in length, respectively. In the present paper, we report the expression of ypGH cDNA in insect cells and the effect of this baculovirus-produced rGH on the growth rate of tilapia (*Oreochrimos niloticus*).

Materials and Methods

Virus and Cells

The insect cell line *Spodoptera frugiperda* 21-AE (Sf21-AE: Summers and Smith 1987) was propagated at 28°C in a spinner culture using TNM-FH medium (Corsaro and Fraser 1988) supplemented with 8% fetal bovine serum. The wild-type *Autographa californica* nuclear polyhedrosis virus (AcMNPV: Smith and Summers 1978) and recombinant virus stocks were grown and titrated in confluent monolayers of Sf21-AE cells.

Construction of Expression Vector

The full length of ypGH cDNA recovered by digestion of pUCGH1 (Tsai et al. 1993) with *Eco*RI was ligated to the *Eco*RI-cut AcMNPV transfer vector, pAcT7 (Lo et al. 1990). pAcT7 (5.3 kilobase pairs (kb)) contains (1) a 2.1-kb truncated *Sph*I to *Bam*HI restriction fragment of the *Eco*RI-cut AcMNPV segment I (7.3 kb), in which the coding region of polyhedrin is removed from the *Bam*HI site to the adenine of ATG (initiation codon), (2) a polylinker derived from pUC19, and (3) a 0.6-kb truncated *Hin*dIII to *Hin*dIII restriction fragment of AcMNPV *Eco*RI fragment, in which the coding region of polyhedrin was partially removed from the 5′ end of *Hin*dIII site to a position near the *Kpn*I site. In brief, pAcT7 consists of a polyhedrin promoter, a multiple cloning site, one fourth of the coding region of the polyhedrin gene, and its 3′ downstream sequences with polyadenylation signal.

There are two internal *Pst*I sites within the ypGH cDNA, located at +206 and +245, respectively. Another *Pst*I site was located at the multiple cloning site of vector. Therefore, if a 0.7-kb and a 5.5-kb fragment were produced after the plasmid construct was digested with *Pst*I, this construct consisted of a right transcription orientation of inserted DNA, with the 5′ end ligated into the downstream of a polyhedrin promoter.

Transfection and Isolation of Recombinant Baculovirus

Spodoptera frugiperda cells were cotransfected with 1 μg of wild-type AcMNPV DNA and 20–30 μg of construct plasmid using the calcium phosphate DNA precipitation method (Burand et al. 1980). Plaques produced from each transfection were screened under the microscope for occlusion minus (Occ^-) cytopathic cells because the polyhedrin gene is inactivated by the insertion of the construct gene (Summers and Smith 1987). Further, the putative recombinant viruses were confirmed by limiting dilution (Carstens et al. 1980) and dot blot hybridization (Pen et al. 1989) with digoxigenin-labeled ypGH cDNA. Positive luminescence clones were identified further by PCR (Innis and Gelfand 1990), using one forward primer, 5′-CTATCAATATATAGTTGCTGATATC-3′ (primer 1; −115 to −91 of polyhedrin gene), and two reverse primers, 5′-GG(T/C)GCGTC(T/G)GG(T/C)GCAAA(T/C)TC(T/C)TT(A/T)AC(T/C)TT(A/G)AA-3′ (primer 2), which derives from the antisense sequence from +713 to +682 of the polyhedrin gene, and 5′-GTCGATGGGGCTG-3′ (primer 3), which derives from the antisense sequence from +289 to +277 of ypGH cDNA.

Analysis of Extracellular Proteins Synthesized by Insect Cells

Sf21-AE cells were infected with parental wild-type baculovirus AcMNPV (Sf21-AE-AcMNPV cells) or the recombinant virus containing the ypGH cDNA (Sf21-AE-AcMNPV-GH cells) at a multiplicity of infection (moi) of 10 pfu/cell. At 96 h postinfection, the infected cultures were harvested, and extracellular proteins were analyzed by SDS-PAGE (Hames 1990) with silver staining (Merril et al. 1981) and by immunochemical reaction after Western blotting (Towbin et al. 1979). Antiserum against natural chum salmon GH was used for the latter procedure.

Cells (6×10^5 per well) in 24-well tissue culture plates were infected with AcMNPV and AcMNPV-GH separately at an moi of 10 pfu/cell and incubated at 28°C for 60 h. Cultures were labeled with 20 μCi of [^{35}S]methionine (1 μCi = 37 kBq) (>1000 Ci/mmol, Amersham) for 6 h. At the end of the labeling period, Sf21-AE, Sf21-AE-AcMNPV, and Sf21-AE-AcMNPV-GH cells were harvested, and the supernatants were analyzed on a 12% SDS polyacrylamide gel. The dried gel was exposed to X-ray film (DuPont) at room temperature for 16 h.

Preparation of Culture Supernatants

Sf21-AE-AcMNPV and Sf21-AE-AcMNPV-GH cells were cultured at 28°C for 4 d in 500 mL of serum-free TNM-FH medium which was prepared by following the formula described by Maiorella et al. (1988). The supernatant saved after centrifugation at 500 × *g* at 4°C was centrifuged at 100 000 × *g* at 10°C for 30 min to remove virions. The supernatant was then concentrated by Amicon ultrafiltration with a YM10 membrane (molecular weight cut off 10 000) at 4°C. The freeze-dried powder of the Sf21-AE-AcMNPV-GH cells supernatant was dissolved in sterile normal saline at a total protein concentration of 0.01, 0.05, or 0.1 μg/μL. Those crude protein preparations contained many proteins in addition to rGH. The Sf21-AE-AcMNPV cells supernatant served as the mock treatment and was prepared at 0.01 μg protein/μL normal saline.

Fish and Rearing Conditions

A total of 50 male tilapia were randomly divided into five groups with an average of 8.38 ± 0.48 g body weight and 7.52 ± 0.38 cm total length. Each group was held indoors and in a separate 100-L holding tank (70 × 50 × 45 cm^3) made of opaque material. Recirculating, filtered dechlorinated water was supplied from a common reservoir equipped with air stones and a temperature controller (23–26°C). Fish were fed once daily with meal powder (crude proteins, 36%; crude lipid, 8%; crude ash, 16%; moisture, 13%; Hanaqua Feed Corporation, Taiwan) at a ration of 3% of total wet weight throughout the experiments.

Assay for Growth-Promoting Activity

Groups of 10 tilapia were injected intraperitoneally with crude proteins obtained from the supernatant of cultured cells once a week. The dosage of proteins was 0.1, 0.5, and 1 μg in 10 μL of 0.9% NaCl per fish. Two additional groups were used as controls. The mock treatment group received an injection of 0.1 μg of the Sf21-AE-AcMNPV supernatant in 10 μL of 0.9% NaCl; the other group received no treatment. One tank was used for each treatment. The wet weight, total length, and food consumption of fish were measured weekly. Percent weight gain over initial weight was calculated as $(WT - wt) \cdot wt^{-1} \cdot 100$ where wt and WT are the initial and final wet weight, respectively. Feed efficiency rate was calculated as [wet weight gain (grams)]·[dry feed intake (grams)]$^{-1}$·100. Condition factor was calculated as $W \cdot L^{-3} \cdot 1000$ where W is wet weight (grams) and L is total length (centimetres). All formulae are described in Takeuchi (1988), and they were calculated after the termination of the 5-wk treatment.

Results

Plasmid Construct and Isolation of Recombinant Baculovirus

The scheme for plasmid construction is outlined in Fig. 1. The resultant plasmid pHM of 6.2 kb contained a 0.9-kb ypGH cDNA insert with the correct orientation for transcription because it generated 0.7- and 5.5-kb *Pst*I fragments. DNA from Sf21-AE-AcMNPV-GH cells generated 1.2- and 0.4-kb fragments when primer 1 and primer 2, or primer 1 and primer 3, were used for PCR, respectively. These two resultant DNA fragments, 1.2 and 0.4 kb, also reacted positively with digoxigenin-labeled ypGH cDNA.

SDS-PAGE and Immunochemical Detection

Supernatants prepared from Sf21-AE, Sf-AE-AcMNPV, and Sf21-AE-AcMNPV-GH cells were analyzed by SDS-PAGE. A protein band with an estimated size of 22 kDa that migrated in a manner similar to that of the native GH was detected in Sf21-AE-AcMNPV-GH cells (lane 1 of Fig. 2A) whereas this band was absent either in the supernatant of uninfected Sf21-AE cells or in that of AcMNPV infected cells (lanes C and W of Fig. 2A). Immunoblot analysis showed that this band reacted specifically with an antiserum against native chum salmon GH (lane 1 of Fig. 2B). Again, this band was not detected in the other samples (lanes C and W of Fig. 2B).

The proteins in the supernatant after culturing the Sf21-AE-AcMNPV-GH-infected cells at 28°C for 4 d were resolved on the gel, and the intensities of the stained protein bands were scanned with a densitometer. The results showed that the quantity of rGH produced by these recombinant baculovirus-infected cells ranged from 2 to 8% of the total proteins in the supernatant from batch to batch.

Radiolabeled Protein Analysis

Proteins in cell culture supernatants after 6 h of labeling with [^{35}S]methionine were analyzed. A protein band of 22 kDa was only seen in the sample from Sf21-AE-AcMNPV-GH cells (lane 1 of Fig. 3) whereas this 22-kDa protein was not detectable in the supernatants of Sf21-AE and Sf21-AE-AcMNPV cells (lanes C and W of Fig. 3).

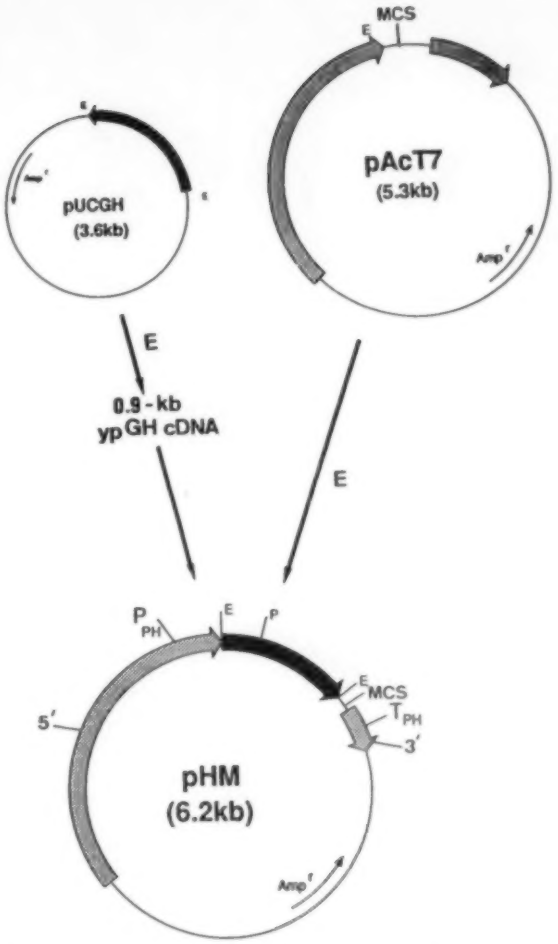

FIG. 1. Construction of expression plasmid. pUCGH1 contained 915 bp of ypGH cDNA insert (dark-stippled arrow). The 5′- and 3′- noncoding region of the polyhedrin gene (light-stippled arrows) are indicated by 5′ and 3′, respectively. Arrows indicate the orientation of the genes. Amp^r, ampicillin resistant gene; E, *Eco*RI; P, *Pst*I; MCS, multiple cloning site (*Sst*I, *Kpn*I, *Sma*I, *Bam*HI, *Xba*I, *Pst*I, *Sph*I); P_{PH} and T_{PH}, promoter and transcription terminator of the polyhedrin gene, respectively. The immediate upstream sequence of the *Eco*RI cloning site in pAcT7 is 5′-TAAAAAAACCTATAATA-3′.

Effects of rGH Treatment on Fish Growth

To determine whether rGH produced by the baculovirus system was biologically active, we injected tilapia with the crude proteins obtained from the supernatant of cell culture Sf21-AE-AcMNPV-GH. This administration led to significant growth enhancement that was evident after the third week of treatment (Fig. 4A). The baculovirus-synthesized rGH was active in this assay at all concentrations (0.1, 0.5, and 1 μg/fish) tested. The increase in wet weight was 54, 48, and 33% higher than that of control groups (mock treated and untreated), respectively. These data show that higher doses led to lower growth rates.

After termination of treatment (at week 5), test and control

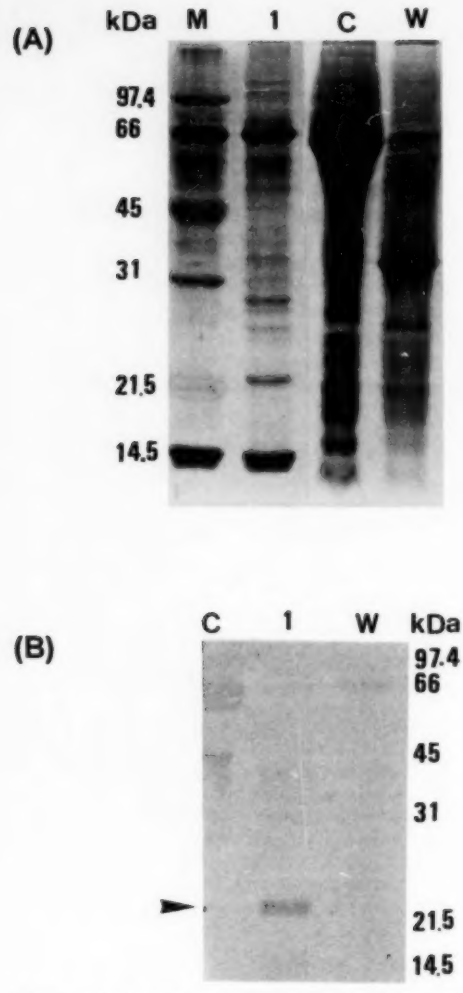

FIG. 2. Proteins in the cell culture supernatants were analyzed by (A) 12% SDS polyacrylamide reducing gel with silver stain and (B) immunochemical reaction. Sf21-AE insect cells (lane C) were infected with parental wild-type baculovirus AcMNPV (lane W) or with recombinant virus containing ypGH cDNA, AcMNPV-GH (lane 1). Antiserum against native chum salmon GH was used for immunological detection. M, marker proteins.

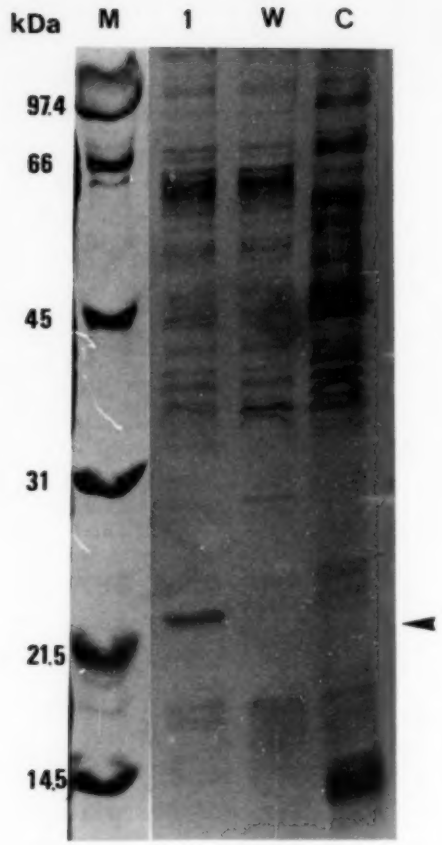

FIG. 3. SDS-PAGE analysis of rediolabeled proteins in cell culture supernatants. Sf21-AE insect cells (lane C) were infected with parental wild-type baculovirus, AcMNPV (lane W), or recombinant virus containing ypGH cDNA, AcMNPV-GH (lane 1). After labeling with [^{35}S]methionine, the cells were harvested and their supernatant proteins run on the gels. M, marker proteins. The arrowhead indicates the position of rGH.

fish showed a statistically significant difference ($p < 0.01$) in weight gain (Table 1). A dosage of 0.1 μg/wk per fish was sufficient to stimulate a significant increase in weight. Similarly, the overall length increases for the 0.1-, 0.5-, and 1-μg dosage groups were 41, 34, and 39%, respectively, and for mock treated and untreated groups were 20 and 25%, respectively (Fig. 4B). Significant differences in final length were observed between test and control groups ($p < 0.01$). However, no significant differences were revealed among the three test groups or between the two control groups.

The overall feed efficiency rates and condition factors of the groups of tilapia injected with rGH-containing protein mixtures are listed in Table 1. The rGH treatment enhanced the feed efficiency rate of fish tested. The food conversion efficiency rate of the 0.1-μg dosage group was as much as twofold greater than that of control groups. At the beginning of the experiment, there were no differences in condition factor among the various groups. Condition factor decreased in all groups over the course of the experiment. There were no significant differences in condition factor between the test and control groups.

Increased growth rates in rGH-treated fish continued for at least 2 wk after the termination of treatment. After week 7, the wet weight and total length for the 0.1-, 0.5-, and 1-μg dosage groups increased to 23 ± 4.73 g and 11.17 ± 0.74 cm, 21.6 ± 4.11 g and 10.86 ± 0.52 cm, and 19.28 ± 2.77 g and 10.66 ± 0.44 cm, respectively. On the other hand, the control groups had wet weights and total lengths of 13.25 ± 1.03 g and 9.38 ± 0.41 cm (the mock treated group) and 13.18 ± 1.56 g and 9.52 ± 0.4 cm (the no-treatment group).

Discussion

Recombinant GH with a molecular weight of 22 kDa, similar to that of the authentic fish GH (Kawauchi et al.

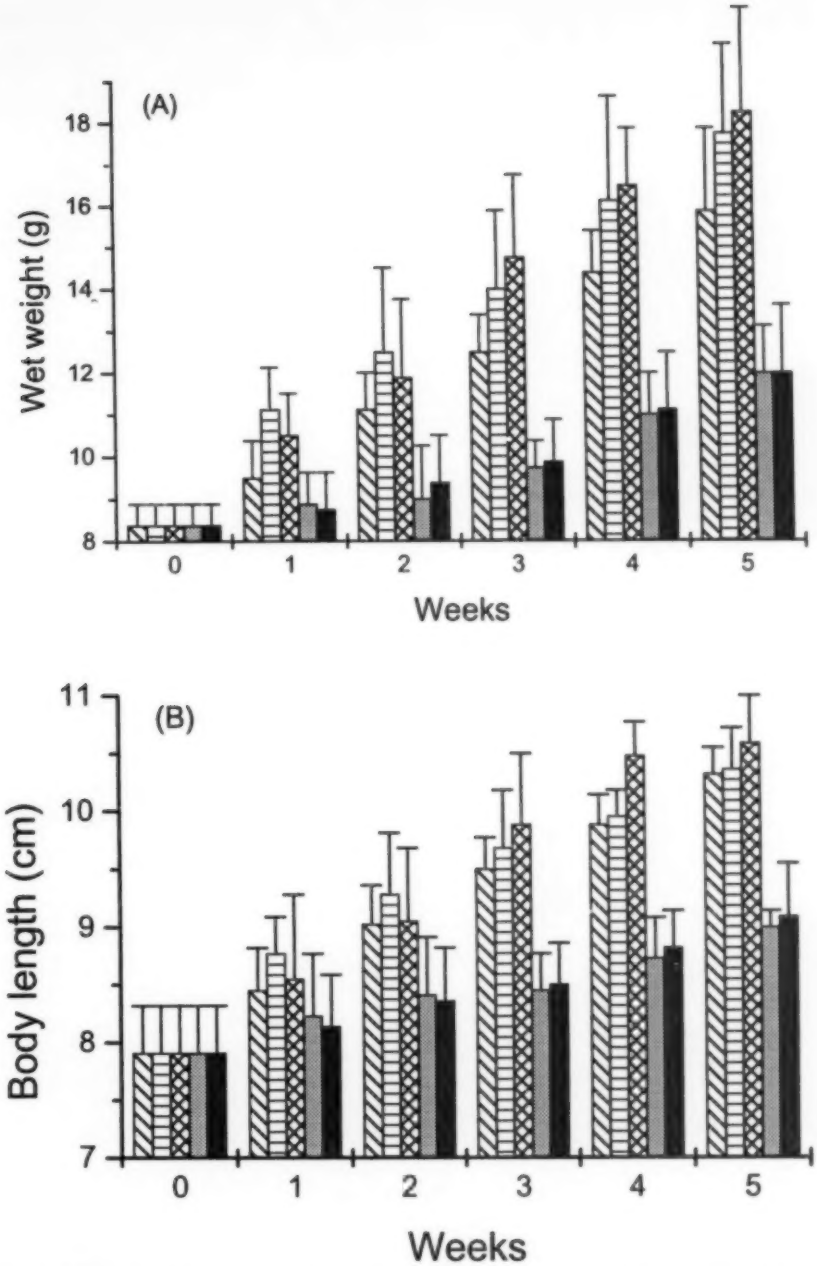

FIG. 4. Effect of injection of baculovirus-produced rGH on the (A) wet weight and (B) total length of tilapia over a 5-wk period. Three doses of crude supernatant of Sf21-AE-AcMNPV-GH cells at a total protein concentration of 1 μg (left-hatched bars), 0.5 μg (horizontally hatched bars), and 0.1 μg (cross-hatched bars), were injected intraperitoneally once a week. The mock treated group (light-stippled bars) received an injection of crude supernatant of Sf21-AE-AcMNPV cells at 0.1 μg of total proteins. Another control group received no treatment (dark-stippled bars). Wet weights and total lengths are shown as mean ± SD (n = 10).

1986; Noso et al. 1988), was detected in the supernatant of the Sf21-AE cells infected by the recombinant baculovirus containing the ypGH cDNA. These results show that rGH was secreted by the Sf21-AE-AcMNPV-GH cells. Moreover, we demonstrated that the rGH biosynthesized by these insect cells had biological activity. The most effective dosage of rGH-containing crude extract produced by the baculovirus expression vector system for enhancement of the growth

TABLE 1. Effect of rGH-containing crude protein mixtures on percent weight gain over initial weight (*G*), feed efficiency rate (FER), and condition factor (CF) of tilapia for overall 5-wk treatments. Data are shown as the average of 10 fish in each treatment. The amount of total crude supernatant protein containing rGH injected in each case is given. Asterisks indicate that the value is significantly different ($p < 0.01$) from the control groups.

Treatment	*G* (%)	FER (%)	CF
Uninjected	47.8	39	15.9
Mock treated	44.2	37	16.3
rGH			
0.1 μg	120.0**	78**	15.4
0.5 μg	112.0**	69**	15.8
1 μg	92.2**	66**	14.5

rate of tilapia was 0.1 μg/fish. This dose is much lower than those used for injecting *E. coli* produced rGH into rainbow trout (*Oncorhynchus mykiss*, previously *Salmo gairdneri*) (1 μg/g fish, Agellon et al. 1988) and snapper (*Pagrus major*) (1.5 μg/g fish, Sato et al. 1988a).

Compared with the growth enhancement of tilapia injected with 0.1 μg/fish, higher doses of rGH-containing crude extract (0.5 and 1 μg/fish) resulted in lower levels of growth stimulation. These adverse effects caused by higher dosage treatment were also observed by Agellon et al. (1988), who reported that the specific growth rate of rainbow trout injected with a high-dose of *E. coli* produced rGH (2 μg/g) was lower than that of a low-dose group (0.2 μg/g). By contrast, adverse reactions to GH treatment have not been reported for GH-treated coho salmon (*Oncorhynchus kisutch*) (Gill et al. 1985). Thus, it would be interesting to study whether or not the adverse result caused by higher doses in this experiment is due to the toxic effects of other proteins in the crude preparation from insect cells.

We observed that the growth rates in rGH-treated fish were continuously increased after the termination of treatments. These results support earlier observations of rGH-treated rainbow trout (Agellon et al. 1988) in which the growth enhancement of rGH-treated fish continued after cessation of treatment. This was perhaps due to either the increased stability of the chimeric GH or the inefficient clearance of exogenous GH from the serum.

The feed efficiency of the rGH-treated groups was significantly greater than that of the control groups, with the 0.1-μg dosage resulting in the highest value (Table 1). We suggest that the improvement of feed efficiency may play an important role in enhancing the growth rate in groups treated with rGH.

The change in condition factor was another notable observation. There was no difference in condition factor between the rGH-treated groups and the controls throughout the experiment. The three dosages of rGH-containing crude extract also resulted in a significant increase in weight and length. This result was not observed in GH-treated coho salmon (Higgs et al. 1975; Gill et al. 1985). In these latter studies the condition factor of treated fish was reduced, with the GH-treated fish growing faster in length than in weight relative to the control. On the other hand, injection of *E. coli* produced rGH into rainbow trout at dosages of 0.2 and 1.0 μg/g fish caused the condition factor to increase (Agellon et al. 1988). These GH-treated rainbow trout showed a more significant increase in weight than in length, perhaps explained by some modification of the activities of rGH. However, this phenomenon was not observed in the present experiments either. These controversial results may be due to the species, physiological stages, and/or season during which the experiments were conducted. In addition, it will be interesting to conduct further studies to determine whether the rGH produced by baculovirus differs in terms of biochemical properties and biological activities compared with that produced by *E. coli* or yeast.

There are four cysteine residues in mature mammalian GH that form two disulfide linkages that determine the configuration of the protein molecule and maintain biological activity (Dayhoff et al. 1978; Lewis et al. 1980; Paladini et al. 1981). The cysteine residues in mature GHs of 16 fish species have been shown to be located at positions nearly identical to those for mature GH of bullfrog, sea turtle, chicken, and various mammals (Watanabe et al. 1992). The locations of the cysteine residues in mature GH of the yellowfin porgy in this study are in agreement with this conclusion (Tsai et al. 1993a). Therefore, the disulfide linkages of fish GH may play a biological role in protein folding identical to that of mammalian GH. Here we have demonstrated that the rGH secreted by the AcMNPV-GH-infected Sf21-AE cells without undergoing renaturation had the ability to enhance the growth rate of the treated fish. This shows that, most probably, the rGH produced by the baculovirus expression vector system is folded properly.

Using the baculovirus expression vector system to produce rGH has advantages over the conventional *E. coli* expression system. Firstly, the baculovirus expression vector system does not require tedious procedures for lysis of the cells, isolation of inclusion bodies, and renaturation of rGH. Secondly, the large-scale purification of the active form of rGH produced extracellularly by the baculovirus expression vector system may be accomplished more easily than that of rGH produced by *E. coli* cells. Furthermore, the crude tissue culture supernatant could be used directly in small quantities to enhance the growth of fish. This approach may be particularly useful in the application of rGH to aquaculture.

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Northern Squawfish, *Ptychocheilus oregonensis*, O_2 Consumption Rate and Respiration Model: Effects of Temperature and Body Size

Joseph J. Cech, Jr.

Department of Wildlife and Fisheries Biology, University of California, Davis, CA 95616, USA

Daniel T. Castleberry[1]

Department of Wildlife and Fisheries Biology, University of California, Davis, CA 95616, USA
and
Columbia River Field Station, National Fisheries Research Center, U.S. Fish and Wildlife Service, Star Route, Cook, WA 98605, USA

Todd E. Hopkins[2]

Department of Wildlife and Fisheries Biology, University of California, Davis, CA 95616, USA
and
Columbia River Field Station, National Fisheries Research Center, U.S. Fish and Wildlife Service, Star Route, Cook, WA 98605, USA

and James H. Petersen

Columbia River Field Station, National Fisheries Research Center, U.S. Fish and Wildlife Service, Star Route, Cook, WA 98605, USA

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Northern squawfish, *Ptychocheilus oregonensis* (live weight range 0.361–1.973 kg), O_2 consumption was measured with temperature-controlled, flow-through respirometers for >24 h. Mean standard O_2 consumption rate of northern squawfish increased with acclimation temperature: 24.3, 49.1, 75.0, and 89.4 $mg \cdot kg^{-0.67} \cdot h^{-1}$ at 9, 15, 18, and 21°C, respectively. Q_{10} analysis showed that O_2 consumption rate temperature sensitivity was greatest at the intermediate acclimation temperatures (15–18°C, Q_{10} = 4.10), moderate at the lower acclimation temperatures (9–15°C, Q_{10} = 3.23), and lowest at the higher acclimation temperatures (18–21°C, Q_{10} = 1.80). Overall Q_{10} was 2.96 (9–21°C). Body size (W, grams) and temperature (T, degrees Celcius) were related to O_2 consumption (M'_{O_2}, grams per gram per day) by $M'_{O_2} = 0.00165\ W^{-0.285} \cdot e^{0.1057T}$. Northern squawfish red to white muscle ratios significantly exceeded those of rainbow trout, *Oncorhynchus mykiss*, in cross sections at 50 and 75% of standard length. High metabolic rates and red to white muscle ratios argue for comparability of northern squawfish with active predators such as sympatric rainbow trout.

Nous avons mesuré la consommation d'O_2 chez la saugagesse du nord, *Ptychocheilus oregonensis* (fourchette de poids vif : 0,361–1,973 kg) pendant plus de 24 h avec des respiromètres à température contrôlée et à écoulement continu. La consommation moyenne standard d'O_2 par la sauvagesse du nord augmentait avec la température d'acclimatement : 24,3, 49,1, 75,0 et 89,4 $mg \cdot kg^{-0,67} \cdot h^{-1}$ respectivement à 9, 15, 18 et 21 °C. L'analyse de Q_{10} a montré que la sensibilité à la température de la consommation d'O_2 était au maximum aux températures intermédiaires d'acclimatement (15–18 °C, Q_{10} = 4,10), modérée aux températures d'acclimatement plus basses (9–15 °C, Q_{10} = 3,23) et au plus bas aux températures d'acclimatement plus élevées (18–21 °C, Q_{10} = 1,80). La valeur globale de Q_{10} était 2,96 (9–21 °C). La taille du corps (W, grammes) et la température (T, degrés Celsius) étaient liées à la consommation d'O_2 (M'_{O_2}, grammes par gramme par jour) selon la formule : $M'_{O_2} = 0,00165\ W^{-0,285} \cdot e^{0,1057T}$. Les rapports des muscles rouges aux muscles blancs chez la sauvagesse du nord dépassaient nettement ceux qu'on observe chez la truite arc-en-ciel, *Oncorhynchus mykiss*, dans des coupes pratiquées à 50 et 75 % de la longueur standard. Le métabolisme élevé et le rapport des muscles rouges aux muscles blancs justifient la comparaison de la sauvagesse du nord à certains de ses prédateurs actifs comme la truite arc-en-ciel, espèce sympatrique.

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The northern squawfish, *Ptychocheilus oregonensis*, is a predaceous cyprinid fish inhabiting freshwater habitats in Oregon, Washington, British Columbia, and Alberta (Scott and Crossman 1973). Squawfish predation on juvenile salmonid fishes in the heavily modified Columbia River system has stimulated research on squawfish bioenergetics,

[1]Present address: Dixon Field Station, National Fisheries Contaminant Research Center, U.S. Fish and Wildlife Service, 6924 Tremont Road, Dixon, CA 95620, USA.

[2]Present address: University of Miami, Rosenstiel School of Marine and Atmospheric Science, Division of Marine Biology and Fisheries, 4600 Rickenbacker Causeway, Miami, FL 33149-1098, USA.

including the construction of models to estimate their predatory consumption (Petersen et al. 1990; Rieman and Beamesderfer 1990). An important component of bioenergetic models is the standard metabolic rate, the basal energy requirement for body maintenance (reviewed by Fry 1971 and Brett and Groves 1979). Such data on the northern squawfish are currently lacking.

Our objective was to determine O_2 consumtpion rates, as measures of standard respiratory metabolic rates, for adult northern squawfish at temperatures spanning the summer conditions (9–21°C) in the Columbia River. We compared northern squawfish O_2 consumption rates with literature values for other cyprinids and with other predaceous freshwater teleosts. Because we found metabolic similarities to the well-studied rainbow trout, *Oncorhynchus mykiss*, we compared red to white muscle ratios between northern squawfish and rainbow trout.

Materials and Methods

Fish Capture and Holding

Adult northern squawfish were collected by electrofishing in the Columbia River near the Bonneville Dam on June 14, 1990. Fish were quickly transported in oxygenated tanks to the USFWS Columbia River Field Station. Fish were held in circular tanks (1.2 m in diameter, 1400 L) for >3 wk at acclimation temperatures of 9, 15, 18, or 21°C. Tanks received a continuous inflow of water from the Little White Salmon River, a tributary of the Columbia River. Only three temperatures could be maintained at one time, so fish were randomly assorted, by weight class, into 9, 15, and 21°C acclimation groups. The 18°C group of fish consisted of the remaining northern squawfish and did not include as broad a range of weights as the other temperature groups. Mean weights (with ranges and number of fish) were 1123 (443–1973 g, n = 18) at 9°C, 1055 (361–1856 g, n = 16) at 15°C, 1190 (958–1494 g, n = 16) at 18°C, and 944 (444–1602 g, n = 14) at 21°C. Standard lengths were 38 (29–46 cm) at 9°C, 39 (29–47 cm) at 15°C, 42 (39–45 cm) at 18°C, and 40 (32–49 cm) at 21°C. Neither mean weights nor mean standard lengths were significantly different (p < 0.05, ANOVA) among temperature groups. Natural light cycles were maintained and northern squawfish were fed live juvenile salmonids (about 1 prey·d^{-1}). Food was withheld from holding tanks at least 2 d before the start of respiration measurements.

O_2 Consumption Rates

Fish were inserted into appropriately sized, flow-through respirometers (5 or 13 L) for O_2 consumption rate (Mo_2) measurements (reviewed in Cech 1990). Respirometers were situated in 250-L insulated fiberglass water baths which were interconnected with submersible pumps and siphons. Due to time and space constraints, experiments on fish at each acclimation temperature were all conducted within a several-day period. Experiments were conducted in the order 9 (n = 18), 15 (n = 16), 21 (n = 14), and 18°C (n = 16). Water temperature in the baths was regulated by thermostatted (YSI[3] model 72 proportional temperature controllers) glass immersion heaters balanced against a continuous inflow of cold (8°C) water. The water was continuously cleaned by particle filters (Teel model 2P275/2P369) that trapped particles >25 μm. Water from the interconnected baths was pumped in excess to an insulated plastic reservoir incorporating an overflow standpipe that maintained a constant pressure head and flow of water to the respirometers. Outflowing water from the respirometers was split by a Y-fitting into two tubes. One tube incorporated an in-line solenoid valve and led to a manifold with a calibrated O_2 electrode (Nester model 617034); the other tube was suspended 0.5 m above the bath to allow timed collection of water for flow calculations when the solenoids were closed. The O_2 electrode was wired to a Nester digital O_2 meter (model 8500) and stripchart recorder (Soltec model 310). Solenoids were controlled by an electronic sprinkler timer (Toro model EL-12+) such that valves sequentially opened at approximately 9-min intervals, sampling water from respirometers with fish, respirometers without fish (blank controls), and a tube without a respirometer (inflow water). $\dot{M}o_2$ (milligrams per kilogram$^{0.67}$ per hour) and $\dot{M}'o_2$ (grams per gram per day) were calculated using

$$\dot{M}o_2 = (O_2\text{in} - O_2\text{out})(Vw \cdot 60)(1000/M_b)^{0.67}$$

and

$$\dot{M}'o_2 = ([O_2\text{in} - O_2\text{out}]/1000)(Vw \cdot 1440)(1/M_b)$$

where O_2in = inflowing [O_2] (milligrams per litre), O_2out = outflowing [O_2] (milligrams per litre), Vw = water flow (litres per minute), and M_b = live body mass of fish (grams).

Standard (resting) $\dot{M}o_2$ (Fry 1971) was determined by calculating the mean of the two lowest Mo_2 values measured over the >24-h experiment for each fish. This method is consistent with that suggested by Bartholomew (1977). Standard metabolic rates were adjusted to weight$^{0.67}$ to facilitate comparisons with other species (Heusner 1982a, 1982b, 1984, 1985, 1987). Because of unequal variances at different temperatures, mean Mo_2s at each temperature were compared using Kruskal–Wallace nonparametric statistics.

Temperature sensitivity of respiratory metabolism was determined by Q_{10}, calculated (Schmidt-Nielsen 1975) as the antilog from log Q_{10}:

$$\log Q_{10} = (\log R_2 - \log R_1) \cdot 10/(T_2 - T_1)$$

where R_2 and R_1 are mean Mo_2s at temperatures T_2 and T_1, respectively.

Respiration Model

The effect of temperature (T, degrees Celsius) and body size of northern squawfish (W, grams) upon $\dot{M}'o_2$ was evaluated using the following model:

$$\dot{M}'o_2 = \alpha W^{\beta} \cdot e^{\tau T}$$

where α, β, and τ are empirically fit parameters. Parameters were estimated using multiple linear regression and the linearized equation

$$\log_e(\dot{M}'o_2) = \log_e(\alpha) + \beta \log_e(W) + \tau T.$$

The model was evaluated by methods described in Neter et al. (1985).

Red to White Muscle Ratios

Eight each of northern squawfish and rainbow trout were examined for relative red and white axial muscle mass.

[3]Mention of brand names does not imply endorsement by the U.S. Government.

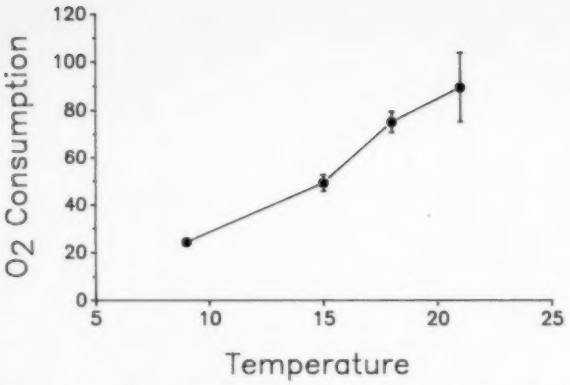

FIG. 1. Mean (±2 SE) standard oxygen consumption rates (mg $O_2 \cdot kg^{-0.67} \cdot h^{-1}$) of northern squawfish over the 9–21°C temperature range. SE bars are hidden in the mean symbol at 9°C.

Northern squawfish were from the O_2 consumption experiments, while rainbow trout were from the University of California, Davis, trout hatchery. We overanesthetized (MS-222) all specimens, wrapped them tightly in double polyethylene bags in a straight (axial) orientation, and froze them for 10 mo. Specimens were then cross-sectioned at 50 and 75% of the standard length from head to caudal peduncle. Sections were melted slightly by wiping with a wet towel, to enhance red and white muscle color differences, and photographed. Photographic slides were projected onto a Micro Plan II digitizing pad, outlines of the red and white muscle masses were traced with the cursor, and relative red and white muscle areas were computed using a microcomputer. Red muscle fibers that may have been mosaically embedded in the white muscle blocks (Webb 1971) were not detectable, although the aerobic potential of mosaic fibers is not certain (Bone 1978). Relative red muscle areas were divided by relative white muscle areas to calculate the red to white muscle ratio. Ratios among sections and species were compared with Kruskal–Wallis nonparametric statistics.

Results

O_2 Consumption Rates

Mean, standard, mass-independent $\dot{M}O_2$ of northern squawfish increased with increasing acclimation temperature (Fig. 1). Mean (±2 SE) rates were 24.3 ± 2.2 at 9°C, 49.1 ± 6.6 at 15°C, 75.0 ± 8.7 at 18°C, and 89.4 ± 28.6 at 21°C. The increases between 9 and 15°C and between 15 and 18°C were significant (Kruskal–Wallis, $p < 0.05$). Q_{10} analyses (Schmidt-Nielsen 1975) showed that $\dot{M}O_2$ sensitivity was greatest at the intermediate acclimation temperatures (15–18°C, $Q_{10} = 4.10$), moderate at the lower acclimation temperatures (9–15°C, $Q_{10} = 3.23$), and lowest at the higher acclimation temperatures (18–21°C, $Q_{10} = 1.80$). The overall Q_{10} was 2.96 (9–21°C).

Respiration Model

The body size – temperature regression model was highly significant ($p < 0.001$, $R^2 = 0.65$; $n = 64$) and all parameters (α, β, τ) in the model were significant ($p < 0.01$). Parameter estimates (SE) were $\log_e(\alpha) = -6.406$ (0.705), $\beta = -0.285$ (0.099), and $\tau = 0.105$ (0.010). The exponential form of the fitted model was

$$\dot{M}'O_2 = 0.00165W^{-0.285} \cdot e^{0.1057\tau}.$$

Residuals were evenly distributed about zero when plotted against fish mass. The scatter of residuals was slightly greater for the 21°C group of fish than for fish tested at 9–18°C, suggesting greater individual variability or sensitivity at the higher temperature. This reflects the greater variability at 21°C in Fig. 1.

Red to White Muscle Ratios

Northern squawfish mean standard length (41.7 cm) and mean body weight (1.339 kg) were statistically indistinguishable (t-tests, $p > 0.05$) from those (40.0 cm and 1.510 kg, respectively) of the rainbow trout. Mean red to white muscle ratios were significantly (Kruskal–Wallis, $p < 0.05$) greater at both 50 and 75% of the standard length in northern squawfish (means ± SE = 0.0790 ± 0.0100 and 0.1010 ± 0.0068, respectively) than in rainbow trout (0.0479 ± 0.0041 and 0.0776 ± 0.0039, respectively).

Discussion

Northern squawfish $\dot{M}O_2$ temperature sensitivity varied with the acclimation temperature range. Other species have also shown Q_{10} variations through acclimation temperature ranges. For example, MO_2 Q_{10}s for rainbow trout were 3.5 between 4 and 10°C and only 1.7 between 12 and 22°C (Muller-Feuga et al. 1978). Baltz et al. (1982) calculated Q_{10}s ranging from 1.05 (10–15°C) to 3.21 (25–27.5°C) for speckled dace, *Rhinichthys osculus* (Cyprinidae). Utah chub, *Gila atraria* (Cyprinidae), show standard MO_2 Q_{10}s ranging from 2.24 (6–9°C) to 5.05 (12–18°C), as calculated from Rajagopal and Kramer's (1974) data. The sigmoid pattern of northern squawfish $\dot{M}O_2$ (Fig. 1) closely approximates the food consumption curve of juvenile northern squawfish over a similar temperature range (7.9–23.0°C, Vigg and Burley 1991).

Northern squawfish have a higher standard $\dot{M}O_2$ than the two well-studied cyprinids common carp, *Cyprinus carpio* and goldfish, *Carassius auratus*. Beamish (1964) calculated standard $\dot{M}O_2$ of common carp from extrapolation of log $\dot{M}O_2$ at various activity levels to zero activity. Beamish and Mookherjii (1964) used the same technique to calculate standard $\dot{M}O_2$ of goldfish. Although the experimental temperatures do not exactly coincide with those used in our study, both common carp and goldfish appear to have lower standard $\dot{M}O_2$s than northern squawfish (Table 1). Whereas both common carp and goldfish generally inhabit quiet or slowly moving water, are omnivorous, and generally do not chase moving prey such as small fish, adult northern squawfish are predators and may inhabit high-velocity sections of streams or rivers (Scott and Crossman 1973; Moyle 1976; reviewed by Brown and Moyle 1981).

Comparisons with other predatory species show that northern squawfish have $\dot{M}O_2$s similar to those of rainbow trout and walleye, *Stizostedion vitreum*. From the extrapolation technique outlined above, Rao's (1968) and Dickson and Kramer's (1971) data on both wild and hatchery rainbow trout compare well with those for northern squawfish

TABLE 1. Comparative, standard mass-independent O_2 consumption rates ($\dot{M}O_2$, mg $O_2 \cdot kg^{-0.67} \cdot h^{-1}$) for several freshwater fishes at various temperatures (°C) and body weight ranges (g).

Species	Temperature	$\dot{M}O_2$	Weight range	Reference
Common carp	10	7.95	58–480	Beamish 1964
	20	22.45	45–440	
Goldfish	10	7.34	10–450	Beamish and Mookherjii 1964
	12	$\bar{x}$ = 29.02	12–234	
	21	$\bar{x}$ = 44.46	7–381	
Northern squawfish	9	24.30	443–1973	Present study
	15	49.10	361–1856	
	18	75.00	908–1494	
	21	89.40	444–1602	
Rainbow trout	10	$\bar{x}$ = 29.34	85–264	Dickson and Kramer 1971
	15	$\bar{x}$ = 41.90	85–264	
	15	52.39	54–135	Rao 1968
	20	$\bar{x}$ = 54.30	85–264	Dickson and Kramer 1971
Walleye	15	26.47	170–181	Tarby 1981
	20	39.98	170–181	

(Table 1). Tarby (1981) used walleye in acrylic, flow-through respirometers similar to those we used and measured standard $\dot{M}O_2$s similar to those of northern squawfish (Table 1). Both rainbow trout and walleye exist in the Columbia River system, although walleye are not native (Wydoski and Whitney 1979).

The specific regression model used to relate standard respiration to temperature and body size has also been used for minnow, *Phoxinus phoxinus* (Cui and Wootton 1988), alewife, *Alosa pseudoharengus* (Stewart and Binkowski 1986), lake trout, *Salvelinus namaycush* (Stewart et al. 1983), largemouth bass, *Micropterus salmoides* (Rice et al. 1983), and other species. The model explained 65% of the variation in northern squawfish respiratory metabolic rate, and parameters can be directly incorporated into bioenergetic models describing growth and consumption (e.g., Hewett and Johnson 1987).

Coefficients from the $\dot{M}'O_2$ equation for northern squawfish can be compared with similar estimates for large predatory fishes such as largemouth bass (Rice et al. 1983), lake trout (Stewart et al. 1983), coho, *Oncorhynchus kisutch*, and chinook salmon, *O. tshawytscha* (Hewett and Johnson 1987), and northern pike, *Esox lucius*, and muskellunge, *E. masquinongy* (Hewett and Johnson 1987). The body size coefficient (β, −0.285), of the northern squawfish $\dot{M}'O_2$ equation was within the range of β coefficients determined for these large piscivores (−0.180 to −0.355). The intercept of the allometric relationship of northern squawfish (α, 0.00165), however was lower than αs for this group of predators (range 0.00246–0.00835). The intercept parameter α can be interpreted as the respiration rate of a 1-g fish at 0°C. The estimate of α for northern squawfish may differ from other estimates because the smallest fish in our analysis weighed 361 g and our lowest test temperature was 9°C. The predictive equation we have developed may not hold for either small fish or low temperatures. The northern squawfish temperature coefficient, τ, was about two times τ coefficients of lake trout, salmon, and northern pike and muskellunge, suggesting that the northern squawfish respiration rate increases at a more rapid rate, at intermediate to high temperatures (Fig. 1), than occurs in these other species.

From their active lifestyle and relatively high cyprinid standard $\dot{M}O_2$s, one might predict that northern squawfish would have larger red muscle masses (McLaughlin and Kramer 1991). Larger red muscle masses typify more active species (Bainbridge, 1960, 1962), and red muscle has higher tissue O_2 demands than white muscle (Gordon 1968; Lin et al. 1974; Itazawa and Oikawa 1983). Northern squawfish red to white muscle ratios significantly exceeded those of rainbow trout, a sympatric active predator. Hatchery rainbow trout were used for the comparison because they were available. Davie et al. (1986) showed that exercise conditioning for 200 d at 1 body length·s^{-1} increased rainbow trout red muscle mass, compared with nonexercised controls, whereas no differences in white muscle mass were detected in the two groups. If wild rainbow trout in the Columbia River exercise significantly more than our hatchery rainbow trout from a 4-m-diameter tank, our results may have overestimated the northern squawfish – rainbow trout red to white muscle ratio difference.

In conclusion, northern squawfish displayed standard $\dot{M}O_2$s comparable with those of other predatory fishes in its environment and red to white muscle ratios that exceeded those of rainbow trout. Northern squawfish standard $\dot{M}O_2$ increased to varying extents with increasing acclimation temperature. Temperature sensitivity of northern squawfish standard $\dot{M}O_2$ showed a peak at intermediate temperatures (15–18°C), compared with lower (9–15°C) and higher (18–21°C) temperatures. A regression model described the effects of temperature and body size on standard metabolism. Parameters of the northern squawfish model were comparable with published estimates for other species, but the temperature coefficient was about two times the values for other large predators. Future studies are needed to assess the effects of water velocity on swimming abilities of northern squawfish $\dot{M}O_2$.

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Temperature and CO_2 Effects on Blood O_2 Equilibria in Northern Squawfish, *Ptychocheilus oregonensis*

Joseph J. Cech, Jr.

Department of Wildlife and Fisheries Biology, University of California, Davis, CA 95616, USA

Daniel T. Castleberry[1]

Department of Wildlife and Fisheries Biology, University of California, Davis, CA 95616, USA
and
Columbia River Field Station, National Fisheries Research Center, U.S. Fish and Wildlife Service, Star Route, Cook, WA 98605, USA

and Todd E. Hopkins[2]

Department of Wildlife and Fisheries Biology, University of California, Davis, CA 95616, USA
and
Columbia River Field Station, National Fisheries Research Center, U.S. Fish and Wildlife Service, Star Route, Cook, WA 98605, USA

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In vitro blood O_2 equilibrium curves were constructed at 9, 15, 18, and 21°C from temperature-acclimated northern squawfish, *Ptychocheilus oregonensis*. At low P_{CO_2} (<1 mm Hg, 1 mm Hg = 133.32 Pa), P_{50}s generally showed variable increases with temperature from 3.6 mm Hg at 9°C to 8.7 mm Hg at 21°C, leading to whole-blood temperature effects (ΔH, kilocalories per mole O_2) ranging from a low +4.4 at 15–18°C to a peak −21.2 at 18–21°C. High-P_{CO_2} (7.6 mm Hg) conditions decreased blood pH and increased P_{50}s at each temperature (Bohr factor). Bohr factors (Φ) ranged from −0.46 at 21°C to −0.70 at 18°C. Considered together, ΔH and Φ values suggest an optimal temperature range of 15–18°C for hemoglobin O_2 loading and unloading in northern squawfish. Nonbicarbonate buffer values ranged from −10.04 at 21°C to −14.13 at 9°C. Overall, the high O_2 affinities and hyperbolic blood O_2 equilibrium curves of northern squawfish resemble those of other large cyprinids (e.g., common carp, *Cyprinus carpio*, tench, *Tinca tinca*, Sacramento blackfish, *Orthodon microlepidotus*) indicating a better ability to tolerate hypoxic environments than sympatric rainbow trout, *Oncorhynchus mykiss*. High northern squawfish blood O_2 capacities and Φs suggest high aerobic capacity, especially at temperatures <21°C.

Nous avons établi les courbes d'équilibre de O_2 dans le sang, in vitro, à des températures de 9, 15, 18 et 21 °C, chez des sauvagesses du nord, *Ptychocheilus oregonensis*, thermiquement acclimatées. À un faible niveau de P_{CO_2} (< 1 mm Hg, 1 mm Hg = 133,32 Pa), les valeurs de la P_{50} montraient généralement des accroissements variables en fonction de la température, entre 3,6 mm Hg à 9 °C et 8,7 mm Hg à 21 °C, ce qui donnait des effets thermiques sur le sang entier (ΔH, kilocalories par mole d'O_2) allant d'un minimum de +4,4 à 15–18 °C à un pic de −21,2 à 18–21 °C. À un niveau élevé de P_{CO_2} (7,6 mm Hg), on observait une baisse du pH du sang et une hausse des valeurs de la P_{50} à chaque niveau de température (facteur de Bohr). Les facteurs de Bohr (Φ) se situaient entre −0,46 à 21 °C et −0,70 à 18 °C. Prises ensemble, les valeurs de ΔH et de Φ semblent indiquer que la fourchette optimale de températures est de 15 à 18 °C pour l'oxygénation et la désoxygénation de l'hémoglobine chez la sauvagesse du nord. Les valeurs obtenues avec tampon non bicarbonaté allaient de −10,04 à 21 °C à −14,13 à 9 °C. Globalement, la forte affinité pour O_2 et les courbes hyperboliques d'équilibre de O_2 dans le sang chez la sauvagesse du nord ressemblent à celles qu'on observe chez d'autres gros cyprinidés (p. ex. la carpe, *Cyprinus carpio*, la tanche, *Tinca tinca*, le Sacramento blackfish, *Orthodon microlepidotus*) ce qui indique chez cette espèce une meilleure aptitude à tolérer les environnements hypoxiques que chez la truite arc-en-ciel sympatrique, *Oncorhynchus mykiss*. La forte capacité d'oxygénation du sang et les valeurs élevées de Φ chez la sauvagesse du nord semblent indiquer une forte capacité aérobique, particulièrement à des températures inférieures à 21 °C.

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For more than 50 yr, northern squawfish, *Ptychocheilus oregonensis*, has attracted interest because of its reputation as a significant predator on young Pacific salmon, *Oncorhynchus*, in Canadian lakes and rivers (Ricker 1941; Foerster and Ricker 1942). Recently, interest has focused on this fish as a seasonal predator on juvenile salmonids in

[1]Present address: Dixon Field Station, National Fisheries Contaminant Research Center, U.S. Fish and Wildlife Service, 6924 Tremont Road, Dixon, CA 95620, USA.

[2]Present address: University of Miami, Rosenstiel School of Marine and Atmospheric Science, Division of Marine Biology and Fisheries, 4600 Rickenbacker Causeway, Miami, FL 33149-1098, USA.

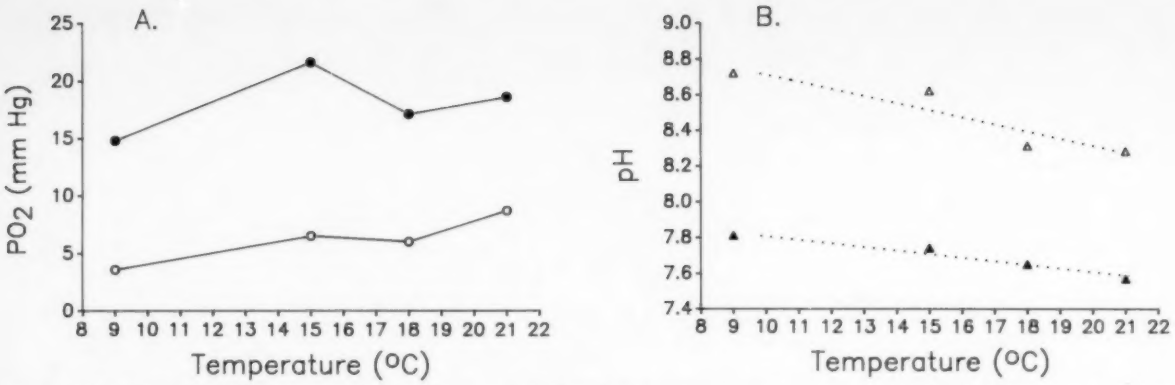

FIG. 1. (A) In vitro relationship between P_{O_2} at 50% saturation (P_{50}) and temperature for northern squawfish low-P_{CO_2} (open circles) amd high-P_{CO_2} (solid circles) blood; (B) in vitro relationship betwen pH and temperature, including least squares regression lines, for northern squawfish low-P_{CO_2} (open triangles) and high-P_{CO_2} (solid triangles) blood.

the highly modified Columbia River system. This interest has resulted in studies of northern squawfish distribution and abundance (Beamesderfer and Rieman 1991), predation (Beamesderfer et al. 1990), dietary habits (Poe et al. 1991), food consumption rates (Vigg et al. 1991), and bioenergetics (Cech et al. 1994). The area of environmental requirements (e.g., with respect to dissolved O_2 and temperature), however, has been largely overlooked. Insights into the species' distributional limits might be gained by studies of its physiological efficiencies and limits regarding abiotic factors such as dissolved O_2 and temperature (Cech et al. 1990).

Studies of blood O_2 equilibria reveal much about a species' environmental limits and efficiencies (reviewed by Riggs 1970; Weber and Wells 1989). Generally, high blood O_2 affinities are found in fishes capable of inhabiting hypoxic environments (reviewed by Burggren et al. 1991). Large Bohr effects typify species capable of high aerobic activity levels (Weber and Wells 1989) or having hyperbolic, blood O_2 equilibrium curves (Jensen 1991). Large blood O_2 capacities are also characteristic of more active fishes (Satchell 1991). Finally, reduced temperature sensitivities have been described for either warm-bodied fishes with countercurrent vascular heat exchangers or fishes that can change thermal environments quickly (Rossi-Fanelli and Antonini 1960; but see Powers et al. 1979). Our objective was to construct blood O_2 equilibrium curves at four temperatures for northern squawfish to help define its environmental requirements and optimal ranges, relative to those of closely related and sympatric species. To our knowledge, this is the first blood O_2 equilibrium study on northern squawfish.

Methods

Fish were collected by electrofishing in the Columbia River and quickly transported to the Columbia River Field Station in oxygenated containers. Fish (approximately 0.5–2.0 kg live weight) were held in aerated, temperature-controlled tanks at either 9, 15, 18, or 21°C for 3–5 wk before use. Dissolved O_2 was maintained at >90% of air saturation in holding tanks. Fish were netted either from their holding tanks or from flow-through respirometers (Cech et al. 1994) and immediately bled from the ventricle using heparinized, 6-mL syringes and 20-gauge hypodermic needles. Only one syringe of blood was removed from each specimen to minimize blood [lactate] and possible harm to the fish. All squawfish survived blood sampling, which took 20–30 s·fish^{-1}.

Well-mixed, pooled blood from five to eight individuals was either loaded immediately (first curve) into two glass rotating tonometers (Hall 1960) or kept in a chilled flask for 60–80 min before being loaded into a second pair of tonometers (second curve). Tonometers were situated in a temperature-controlled water bath at either 9, 15, 18, or 21 ± 0.2°C to match the acclimation temperature of the fish. Hematocrit (percentage after centrifugation for 3 min at 11 000 × *g*) and whole blood [lactate] (millimoles per litre) (YSI model 27 analyzer) were immediately measured on the pooled blood. Tonometer pairs received either humidified air from an air pump and humidified N_2 from a cylinder for low-P_{CO_2} (0.2 mm Hg, 1 mm Hg = 133.32 Pa) curves or humidified gas mixtures (1% CO_2 with either balance air or N_2) from Wostoff gas mixing pumps for high-P_{CO_2} (7.6 mm Hg) curves.

Blood was equilibrated for 50 min, after which samples of oxygenated and deoxygenated blood were withdrawn from the tonometers and mixed in a gas-tight glass syringe with a mixing bead (Edwards and Martin 1966; Scheid and Meyer 1978) for measurements. P_{O_2} (millimetres Hg) was measured for each mixture using a calibrated O_2 analyzer and thermostatted electrode (Radiometer PHM73/E5046/D616); pH was measured for each 50% mixture (Radiometer PHM73/G297/K497). Blood O_2 capacity (CB_{O_2} millilitres per decilitre, O_2 content at 100% saturation) was measured using a Lex-O_2-Con analyzer (Lexington Instruments). Several blood lactate measurements were made to ensure that the blood was not undergoing significant metabolic acidosis, e.g., in the deoxygenated tonometer. The second curves at the two warmer temperatures were each discarded and the temperature conditions subsequently repeated (as first curves from separate groups of fish) because of metabolic acid build-up (indicated as blood [lactate] >1 mmol·L^{-1}). Blood [lactate] for all other curves was 0.1–0.6 mmol·L^{-1}. J.J. Cech, D.T. Castleberry, and T.E. Hopkins (unpublished data) measured a mean blood [lactate] of 0.6 mmol·L^{-1} in resting, undisturbed northern squawfish, when sampled via dorsal

TABLE 1. Northern squawfish hematological characteristics. Temperature in °C, P_{CO_2} in mm Hg, P_{50} = P_{O_2} at 50% saturation (mm Hg), CBO_2 = blood O_2 capacity ($mL \cdot dL^{-1}$), Hct = hematocrit (%), β = whole-blood nonbicarbonate buffer value, Φ = Bohr factor, n_{50} = hemoglobin subunit cooperativity, and ΔH = temperature effect.

Temp.	P_{CO_2}	pH	P_{50}	CBO_2	Hct	β	Φ	n_{50}	ΔH
9	<1	8.72	3.6	13.0	30	−14.13	−0.68	0.81	
9	7.6	7.81	14.8	11.1	30			1.36	−15.9
15	<1	8.62	6.5	12.9	24	−11.74	−0.59	1.25	
15	7.6	7.74	21.6	12.5	24			1.55	+4.4
18	<1	8.31	6.0	12.1	28	−13.68	−0.70	0.83	
18	7.6	7.65	17.1	12.9	31			1.24	−21.2
21	<1	8.28	8.7	10.7	27	−10.04	−0.46	1.11	
21	7.6	7.57	18.6	10.3	27			1.42	

aortic cannula. Black (1955) measured a mean blood [lactate] of 2.13 $mmol \cdot L^{-1}$ in unexercised northern squawfish, when sampled via cardiac puncture.

Bohr factors, temperature effects, and nonbicarbonate buffer values were calculated from various measurements. Bohr factor (Φ), a measure of pH (and CO_2) sensitivity, was calculated from

$$\Phi = \Delta \log P_{50}/\Delta pH$$

where P_{50} (millimetres Hg) is the PO_2 at 50% saturation. Temperature effect (ΔH, kilocalories per mole O_2, a measure of temperature sensitivity) was calculated using a form of the van't Hoff equation:

$$\Delta H = 4.578(\Delta \log P_{50}/\Delta(1/T) \cdot 10^3)$$

where T is temperature (degrees Kelvin) (Wyman 1964; Powers et al. 1979). Whole-blood nonbicarbonate buffer value (β, $\Delta [HCO_3^-]/\Delta pH$) was calculated (Davenport 1974) from

$$\beta = \Delta[HCO_3^-]/\Delta pH.$$

$[HCO_3^-]$ was calculated using pH and P_{CO_2} data in the Henderson–Hasselbalch equation (Davenport 1974) with constants published by Reeves (1976). Hemoglobin subunit cooperativity (n_{50}) was estimated as the slope of Hill plots (i.e., log ($Y/100 - Y$) versus log p where Y = percent saturations between 10 and 90% and $p = P_{O_2}$ (Riggs 1970; Jensen 1991).

We related temperature and pH with a least squares linear regression, and we tested for significant ($p < 0.05$) correlations among all measured and calculated variables with ABstat statistical software.

Results

Temperature Effects

Increases in temperature generally decreased blood O_2 affinity (increased P_{50}) and decreased blood pH (Fig. 1). Higher (absolute value) ΔHs show high temperature sensitivity of northern squawfish hemoglobin O_2 loading/unloading in the 18–21°C range compared with a lower sensitivity in the 9–15°C range (Table 1). Northern squawfish showed a ΔH plateau between 15 and 18°C. Linear regression slopes relating temperature and pH were -0.02 pH unit·$°C^{-1}$ ($r = -0.97$) for 7.6 mm Hg P_{CO_2} and -0.04 pH unit·$°C^{-1}$ ($r = -0.93$) for <1 mm Hg P_{CO_2} (Fig. 1). Neither hematocrit ($p > 0.8$), β ($p > 0.1$), nor Hill's n_{50} ($p > 0.2$) showed significant correlations with temperature (Table 1).

Bohr factor and low-P_{CO_2} CBO_2 varied with temperature. Bohr factor showed a peak at 18°C and a low at 21°C (Table 1). Low-P_{CO_2} CBO_2 showed a decreasing trend with increasing temperature; however, there was no significant correlation ($p > 0.50$) between temperature and CBO_2 overall (Table 1).

CO_2 Effects

Northern squawfish low-P_{CO_2} and high-P_{CO_2} curves at 9, 15, 18, and 21°C are shown in Fig. 2, and Table 1 shows that increases in P_{CO_2} from <1 to 7.6 mm Hg decreased blood pH (negative correlation, $p < 0.01$) and O_2 affinity (positive correlation with P_{50}, $p < 0.01$). Thus, the high-P_{CO_2} curves were all shifted to the right of the low-P_{CO_2} curves (Bohr factor), facilitating the hemoglobins' O_2 unloading at the higher P_{CO_2} and lower pH conditions expected at metabolizing tissue sites and subsequent O_2 loading under low-P_{CO_2} conditions at the gills. Correlation analysis showed no significant relationship ($p > 0.50$) between P_{CO_2} (or pH) and CBO_2 (Root effect).

Discussion

Several characteristics of northern squawfish blood and hemoglobin(s), e.g., high blood O_2 affinities and nonbicarbonate buffer values and low n_{50}s, indicate that they can successfully inhabit hypoxic (and quite possibly) hypercapnic environments, especially at temperatures <21°C. Comparisons of CBO_2 and Bohr effect with those of other species reveal an ability to be aerobically active, especially in the 15–18°C range (Table 2).

Hypoxic and Hypercapnic Environments

The northern squawfish's high O_2 affinity and hyperbolic blood O_2 equilibrium curves (Hill's $\bar{n}_{50} = 1.00$) allow high O_2 saturation of gill blood at low environmental P_{O_2}s (Fig. 2). High O_2 affinity hemoglobins have been linked to tolerance of hypoxic environments in three other cyprinid fishes: the European tench, *Tinca tinca* (Eddy 1973; Jensen and Weber 1982, 1985), the Eurasian common carp, *Cyprinus carpio* (Garey and Rahn 1970), and the North American Sacramento blackfish, *Orthodon microlepidotus* (Cech et al. 1979).

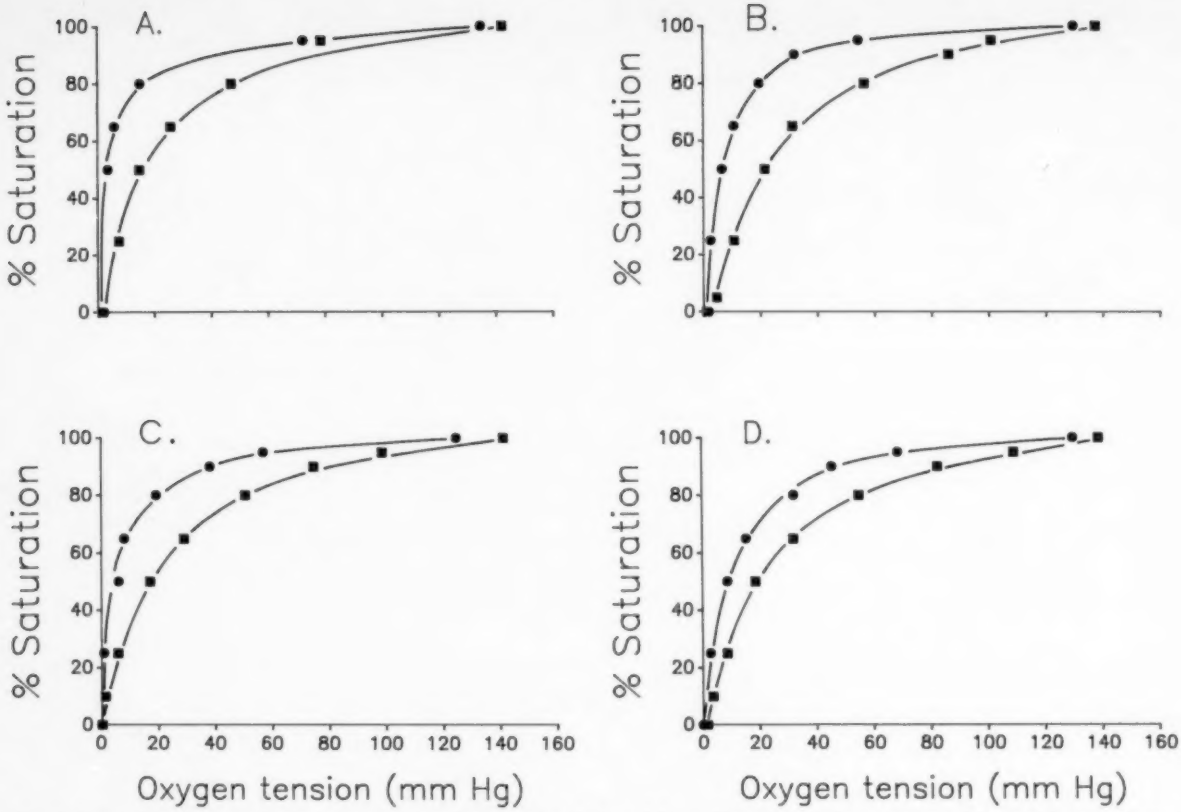

FIG. 2. Whole-blood O_2 equilibrium curves at low-P_{CO_2} (circles, P_{CO_2} = 0.2 mm Hg) and high-P_{CO_2} (squares, P_{CO_2} = 7.6 mm Hg) conditions and at (A) 9, (B) 15, (C) 18, and (D) 21°C. Curves fitted by eye.

Table 2 shows that northern squawfish and other cyprinids have higher blood O_2 affinities than the sympatric salmonid, rainbow (steelhead) trout, *Oncorchynchus mykiss*. All the cyprinids show essentially hyperbolic curves (n_{50} = approximately 1.0), while the rainbow trout shows higher n_{50} values (Table 2). Presumably, their high blood O_2 affinity would permit northern squawfish to saturate their blood with O_2 to acceptable levels while occupying hypoxic microhabitats. However, these microhabitats may not be as hypoxic as those experienced by tench, common carp, or Sacramento blackfish, which primarily dwell in nonflowing, stratifiable systems such as lakes and ponds (Garey and Rahn 1970; Scott and Crossman 1973; Lallatin 1975; Moyle 1976). Dissolved O_2 measurements of Columbia River mainstream and marginal habitats reveal that hypoxia is not as severe as in lakes and ponds (J.H. Petersen, Columbia River Field Station, National Fisheries Research Center, U.S. Fish and Wildlife Service, Star Route, Cook, WA 98605, USA, personal communication), but northern squawfish are also successful inhabitants of many Canadian lakes (Scott and Crossman 1973).

From this comparison, northern squawfish should be capable of saturating its blood to an arterial level (approximately 85 mm Hg P_{O_2}, J.J. Cech, D.T. Castleberry, and T.E. Hopkins, unpublished data) at lower environmental P_{O_2}s than rainbow trout. This is reinforced by rainbow trout's greater n_{50} values, facilitating loading and unloading O_2 more efficiently at higher blood P_{O_2}s, which typify more normoxic environments (Table 2).

Nonbicarbonate buffer values (β) reflect the ability of blood proteins to buffer changes in P_{CO_2} (Davenport 1974; Wood et al. 1977). Northern squawfish βs are comparable with those of common carp, tench, and Sacramento blackfish, reflecting its ability to handle metabolically produced or environmentally increased CO_2, especially at temperatures <21°C (Table 2). Northern squawfish β values were all greater than those of rainbow trout, while Φs were comparable (Table 2), indicating an enhanced ability to tolerate hypercapnia.

Temperature

Fish with temperature-sensitive hemoglobins show temperature-induced facilitation of venous hemoglobin O_2 unloading at tissue capillary beds when temperatures are warm and O_2 demands are increased (see review by Wood 1980). O_2 unloading from the northern squawfish hemoglobin was assisted by the decreased blood pH at increased temperatures (Fig. 1B; Table 1), i.e., from the changing ionization constant of water (Howell et al. 1970). However, the temperature-induced increase in P_{50} may limit O_2 loading at the gills, especially in hypoxic environments (Fig. 2). Decreases in northern squawfish blood pH with increasing temperature were comparable with those measured in larger spotted dogfish, *Scyliorhinus stellaris* (Heisler 1978). Northern

TABLE 2. Comparative blood O_2 equilibrium characteristics. Abbreviations and units as in Table 1.

Species	Temp.	P_{50}	CBo_2	β	Φ	n_{50}	Reference[a]
Rainbow trout	10	9.0					1
Rainbow trout	15	13.2	8.9	−5.05	−0.57	1.82	1, 2
Rainbow trout	20	20.2	9.5	−6.36	−0.59	1.38	1, 2
Northern squawfish	9	3.6	13.0	−14.13	−0.68	0.81	3
Northern squawfish	15	6.5	12.9	−11.74	−0.59	1.25	3
Northern squawfish	18	6.0	12.1	−13.68	−0.70	0.83	3
Northern squawfish	21	8.7	10.7	−10.04	−0.46	1.11	3
Tench	13	2.0	7.7		−0.64		4
Tench	15	6.2	10.2	−14.00	−0.72	1.30	5
Tench	20	3.5	7.7		−0.69		4
Common carp	10	2.0			−1.20		6, 7
Common carp	15			−8.70			8
Common carp	20	7.0	11.0		−0.98		9
Sacramento blackfish	10	<1	9.6	−8.58		0.96	10
Sacramento blackfish	15	2.5	10.6	−10.53	−0.67	1.06	10
Sacramento blackfish	20	3.5	10.3	−11.45	−0.71	1.41	10
Sacramento blackfish	25	3.5	9.2	−15.14	−0.83	0.98	10
Sacramento blackfish	30	11.0	9.9	−9.42	−0.55	0.94	10

[a]1, Cameron (1971); 2, Eddy (1971); 3, present study; 4, Eddy (1973); 5, Jensen and Weber (1982); 6, Garey (1967); 7, Albers et al. (1983); 8, Claiborne and Heisler (1984); 9, Weber and Lykkeboe (1978); 10, Cech et al. (1979).

squawfish mean metabolic O_2 demands are higher at 21°C than at 9, 15, or 18°C (Cech et al. 1994).

However, hemoglobin temperature effects can be modified by intraerythrocytic factors. Powers et al. (1979) argued against forming generalizations among fishes regarding reduced hemoglobin temperature sensitivity in fluctuating thermal environments, due to variations in intracellular pH regulation and organic phosphate concentrations. Jensen and Weber (1987) showed that ATP depresses the temperature sensitivity of tench hemoglobin. In the present study, we did not measure intraerythrocytic phosphate concentrations. However, by using freshly drawn whole blood from temperature-acclimated fish, our in vitro determinations should have been appropriate for wild northern squawfish acclimated to these temperatures.

Northern squawfish blood O_2 equilibria show enhanced temperature independence at temperatures <21°C and particular independence at 15–18°C (Fig. 2B and 2C; Table 1). Interestingly, it is between 15 and 18°C that northern squawfish show the greatest change in O_2 uptake per degree Celsius (Cech et al. 1994). The P_{50} plateau at 15–18°C would exact the lowest blood O_2 "penalty" within the thermal zone where metabolism was increased (e.g., for predatory responsiveness) or decreased (e.g., for increased assimilation of ingested prey) maximally over a small temperature range (Rossi-Fanelli and Antonini 1960; Brett and Groves 1979).

Overall, the 15–18°C range seems to be optimal for northern squawfish O_2 uptake and transport. Below the optimal range, i.e., 9°C, northern squawfish metabolism is very slow for a freshwater predatory fish (Cech et al. 1994). At 5–10°C, mean standard metabolic rates of four comparison predators, rainbow trout, brook trout, *Salvelinus fontinalis*, brown trout, *Salmo trutta*, and striped bass, *Morone saxatilis*, were from 1.82- to 3.44-fold higher than that of northern squawfish at 9°C (Beamish 1964; Rao 1968; Dickson and Kramer 1971; Kruger and Brocksen 1978; Cech et al. 1994). Also, at colder temperatures, northern squawfish hemoglobin is quite temperature sensitive in the 9–15°C range (Table 1, Riggs 1970), and the species' swimming ability is reduced at 12°C (M.G. Mesa, Columbia River Field Station, National Fisheries Research Center, U.S. Fish and Wildlife Service, Star Route, Cook, WA 98605, USA, personal communication). Above the optimal (15–18°C) temperature range, i.e., 21°C, blood O_2 affinity, capacity, and delivery (Φ) and CO_2 buffering ability (β) are all reduced to their lowest levels (Table 1), and food and O_2 consumption rates level off (Vigg and Burley 1991; Cech et al 1994).

Activity

Many aerobically active species have large CBo_2s and Φs, presumably to efficiently transport and unload O_2 to exercising red muscles (Cameron and Davis 1970; Weber and Wells 1989). Extremely active fish such as albacore, *Thunnus alalunga*, have very large CBo_2s (21.8 $mL \cdot dL^{-1}$, Cech et al. 1984). Although northern squawfish CBo_2s are substantially below those of albacore, they actually exceed those of the active rainbow trout (Table 2). Many fish with high Φs tend to be very active. For example, Atlantic mackerel, *Scomber scombrus* (−1.20, Hall and McCutcheon 1938), albacore (−1.17, Cech et al.. 1984), and blue marlin, *Makaira nigricans* (−1.00, Dobson et al. 1986), have some of the highest Φs recorded. Befitting of a predator that feeds at least partially on smaller fish (Poe et al. 1991), northern squawfish Φs are equal to or exceed those of rainbow trout at temperatures <21°C (Table 2). This could enhance tissue site O_2 unloading from hemoglobin and/or contribute to pH and CO_2 homeostasis (Jensen 1991). Larger red muscle masses also characterize active fishes (reviewed by Bone 1978). Northern squawfish have significantly greater red to white muscle ratios in body cross sections than rainbow trout (Cech et al. 1994). From these criteria, northern squawfish should show comparable or superior aerobic performance to rainbow trout. Preliminary data show that northern squawfish (30–39 cm fork length) can swim at 2.7 body $lengths \cdot s^{-1}$ for >1 h at 18°C (M.G. Mesa, Columbia River Field Station, National Fisheries Research Center, U.S. Fish

and Wildlife Service, Star Route, Cook, WA 98605, USA, personal communication). When subjected to a similar regime (60-min test periods), rainbow trout ("length" = 29.2 cm) swam at a maximum 2.0 body lengths·s^{-1} at 15°C (Webb 1971). Webb's (1971) rainbow trout were obtained from a hatchery and may have exhibited reduced development of swimming musculature, depending on relative exercise conditioning regimes in the hatchery compared with natural environments such as the Columbia River (Davie et al. 1986).

In conclusion, the northern squawfish displays blood O_2 equilibrium characteristics that resemble those of other cyprinid fishes but that include a more hyperbolic curve and higher O_2 affinities and nonbicarbonate buffer values than those of rainbow trout. These characteristics lead to an enhanced ability to tolerate hypoxic and hypercapnic environments compared with sympatric rainbow trout. In addition, high blood O_2 capacities and Bohr factors allow northern squawfish to be aerobically active, especially at temperatures <21°C. Finally, northern squawfish blood shows a maximal Bohr factor at 18°C and a minimal temperature effect at 15–18°C, which is suggested as an optimal temperature range. Temperature effects on northern squawfish critical swimming velocity are currently being investigated.

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Alterations in Aquatic Plant Community Structure following Liming of an Acidic Adirondack Lake

Evan R. Weiher[1] and Charles W. Boylen[2]

Department of Biology and Fresh Water Institute, Rensselaer Polytechnic Institute, Troy, NY 12180-3590, USA

and Paul A. Bukaveckas

Institute for Ecosystem Studies, Box AB, Millbrook, NY 12545, USA

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The changes in the macrophyte community composition of Woods Lake, New York (Adirondack Region), following lake neutralization with calcite are described with reference to the immigration and extirpation of species. Seven new species were found after calcite addition; one of these, *Potamogeton epihydrus*, became the single most abundant species within the lake. Two species were extirpated from the lake (*Sphagnum* sp. and *Utricularia geminiscapa*) within 5 yr following the initial treatment. Overall plant coverage decreased from 47.6 to ~20% of the lake surface area. This decrease was due in large part to the decline of the previously dominant *Utricularia purpurea*. Expansion of floating-leafed species and a canopy-forming pondweed (*P. epihydrus*) signifies a shift in community structure towards that characteristic of unperturbed circumneutral lakes. Specific responses of neutralization were often not consistent with the known physiological ecology or biogeographic distribution of species.

Les modifications dans la composition de la communauté de macrophytes du lac Woods, New York (région des Adirondacks), après neutralisation du lac par application de calcite sont décrites relativement à l'immigration et à la disparition des espèces. Après addition de calcite, sept nouvelles espèces ont été observées; l'une de celles-ci, *Potamogeton epihydrus*, est devenue l'espèce la plus abondante du lac. Deux espèces ont disparu (*Sphagnum* sp. et *Utricularia geminiscapa*) au cours des 5 ans qui ont suivi le traitement initial. La couverture végétale est passée de 47,6 % à environ 20 % de la superficie du lac. Cette diminution était attribuable en partie à la baisse de l'espèce qui autrefois prédominait, c'est-à-dire *Utricularia purpurea*. L'étalement d'espèces à feuilles flottantes et la présence d'un potamot formant un tapis (*P. epihydrus*) correspondent à une évolution de la structure de la communauté vers une communauté caractéristique de lacs non perturbés presque neutres. Les réactions particulières à la neutralisation étaient souvent non conformes à l'écologie physiologique ou à la répartition biogéographique connue des espèces.

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Surveys of aquatic plant vegetation among lakes representing a pH gradient have suggested that lake acidification is accompanied by pronounced changes in macrophyte community structure. Acidic lakes exhibit lower diversity relative to circumneutral lakes of similar size (Roberts et al. 1985). Reductions in diversity associated with decreasing pH have been described as a progressive disappearance of species without apparent replacement (Jackson and Charles 1988). In North America, the generalized community structure of clearwater acidic lakes includes nearshore mixed isoetids (including *Eriocaulon septangulare* and *Lobelia dortmanna*) and some *Sphagnum*, often with dense beds of *Utricularia purpurea* at greater depths (Roberts et al. 1985). Acidic lakes generally lack the well-developed patterns of depth zonation common to circumneutral lakes. A floating-leafed zone is not generally evident in acidic lakes, although scattered nymphaeids are usually present. Acidic lakes are often without caulescent, canopy-forming plants such as the magnopotamids and myriophyllids (sensu Hutchinson 1975) that are common in circumneutral lakes (Robert et al. 1985; Hunter et al. 1986; Jackson and Charles 1988). Long-term observations of aquatic plant communities in Europe have revealed that lake acidification is often associated with the spread of *Sphagnum* and/or *Juncus bulbosus* into areas previously inhabited by mixed isoetids (Roelofs 1983; Grahn 1986). In North America, no long-term data exist that document aquatic plant community changes, but observational studies along pH gradients indicate no spread of *Sphagnum* or *J. bulbosus* (a rare species in Canada, Argus and Pryer 1990).

The addition of lime (CaO) or calcite ($CaCO_3$) to acidic lakes is commonly used as a management technique to improve water quality and thereby mitigate the effects of acidification on aquatic biota. In Europe, lake liming has been associated with declines in *J. bulbosus* and *Sphagnum* and an increase in the abundance of isoetids (Hultberg and Andersson 1982; Eriksson et al. 1983). Eriksson et al. (1983) noted that in two of four lakes, *Potamogeton natans* became established, and Hultberg and Andersson (1982) noted that a *Potamogeton* sp. "responded positively" to liming.

[1]Present address: Department of Biology, University of Ottawa, ON K1N 6N5, Canada.

[2]Author to whom correspondence should be addressed.

In this paper, we describe the changes in submersed and floating-leafed macrophytes following the liming of an acidic Adirondack lake (Woods Lake). Calcium carbonate was added to Woods Lake in 1985 and 1986 and to two catchments in the Woods Lake watershed in 1989 to maintain a circumneutral pH during the period from 1985 to 1991 (see Porcella 1989 for an overview of the Lake Acidification Mitigation Project). Prior to liming, the aquatic plant community of Woods Lake was similar to that of other acidic Adirondack lakes, with dense beds of *U. purpurea* accounting for most of the plant biomass (Roberts et al. 1985). A significant decrease in the biomass and coverage of *U. purpurea* was observed following calcite addition (Bukaveckas 1988) and was attributed to the decrease in light availability during the postliming period (Bukaveckas and Driscoll 1991). The objectives of this paper were to analyse changes in species composition and to test the hypothesis that lake liming results in a shift in community characteristics similar to those observed in nonacidic Adirondack lakes.

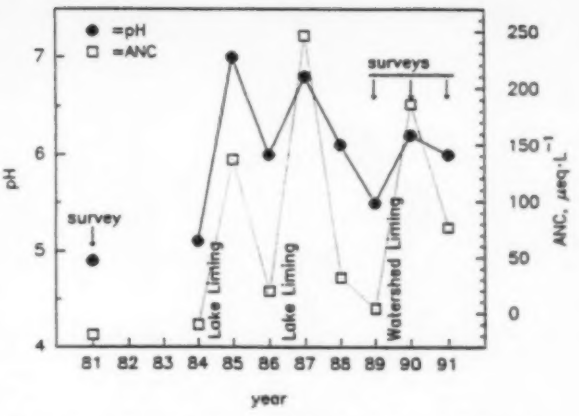

FIG. 1. May–September mean pH levels, acid-neutralizing capacity, and calcite applications to Woods Lake, New York. Arrows indicate aquatic plant surveys.

Methods

Study Site and Treatment Design

Woods Lake is located in the west-central Adirondack Mountains in a predominantly forested and undeveloped watershed. It has a surface area of 23 ha, a mean depth of 3.5 m, a maximum depth of 12 m, and a hydraulic residence time of 214 d (Bukaveckas 1989). Prior to liming, the chemical characteristics of Woods Lake were typical of clearwater acidic lakes in the Adirondack region (Driscoll and Newton 1985). Sulfate was the dominant anion, and the equivalence of acidic anions exceeded base cations resulting in low pH (4.9 to 5.2), low acid-neutralizing capacity (-15 to $+5$ $\mu eq \cdot L^{-1}$), and generally high concentrations of aluminum, predominantly as the labile (monomeric) fraction (Driscoll et al. 1989). In May 1985, a highly pure calcite slurry (23 t of 98% $CaCO_3$) was applied by the helicopter on a volumetric basis to achieve a uniform target pH. A second treatment (35 t) was performed 16 mo later, in September 1986. Thereafter, the lake was allowed to reacidify for three years (Fig. 1). During the fall of 1989, two catchments within the Woods Lake watershed were treated by the addition of 1100 t of $CaCO_3$. Calcite pellets were applied to watershed soils by helicopter to achieve a uniform target distribution of 5–10 $t \cdot ha^{-1}$. Data presented in this paper were collected 4 yr after the first lake liming (pH 5.5 in 1989) and during the first and second years following watershed liming (pH 6.2 in 1990 and 6.0 in 1991). These results are compared with similar data collected prior to the lake and watershed treatments (pH 4.8 in 1981, Roberts et al. 1985).

Vegetation Analyses

The lake bottom was visually surveyed by boat and by divers to map the distribution of all species in the lake. Percent coverage estimates were made from a boat in areas less than 0.5 m in depth, areas from 0.5 to 5 m were surveyed by replicate divers who snorkeled or used air supplied from a "third lung", and areas over 5 m were surveyed using SCUBA. The entire littoral area less than 5 m deep was intensively surveyed (75% of the lake), while the deeper areas received less attention. Surveys generally required 8–10 h, which corresponded to an average rate of 14×14 m observed$\cdot min^{-1}$. Percent coverage estimates were used to produce gridded maps, and the data were first summed over several depth intervals and second over the whole lake. We attempted to follow closely the methods that were used in 1981 (Robert et al. 1985) so that comparisons could be made. Observation- or sampling-unit size was not set to a predetermined size; rather, observations were based on areas that were observed to have similar coverages and where natural boundaries were evident. Where gradients in coverage existed, areas were delineated when the estimated coverage of one species changed by 5–10%. Excluding the areas greater than 5 m deep, mean observation-unit size was 0.194 ± 0.012 ha (SE) or an area approximately 25×78 m. The smallest area unit was 0.03 ha (10×30 m) and the largest was 0.58 ha (50×116 m). Small patches or very diffuse cover within observational areas were scored as present, equal to 1% coverage.

Confidence intervals cannot be put on the percent coverage estimates because they represent sums of weighted averages based on patchy distributions. If the distribution of plants were uniform or expected to be uniform, then confidence intervals could be determined. The uncertainty of the percent coverage estimates represented by between-person errors was about 10% when plant cover within an observational unit was 20% or more. The number of observation units per survey was always over 100; therefore the standard error of the percent coverage estimates is less than 1%. An argument could also be made that because our minimum sample area was 0.03 ha, this was the minimum observable sampling unit, and each larger sample area is simply made up of many 0.03-ha units. This would bring the number of observations to approximately 700, thereby reducing the standard error to <0.4%.

Although estimates of percent coverage are somewhat subjective, this method is particularly well-suited to assessing species richness in small lakes, since the entire lake is censused, rather than sampled by transect lines or quadrats which tend to omit rarer species.

Shannon diversity was calculated as

$$\Sigma[(p_i)\log_2(p_i)]$$

TABLE 1. Percent coverage estimates of aquatic plants in Woods Lake, New York, distributed by plant growth form.

	1981	1989	1990	1991
Total isoetids	6.88	4.45	7.72	7.84
Percent total coverage	14.4	22.8	39.7	34.7
Eriocaulon septangulare With.	4.80	2.57	6.34	3.76
Isoetes sp.	0.04	0.14	0.02	0.03
Juncus pelocarpus Meyer	0.04	0.44	0.47	1.27
Lobelia dortmanna L.	1.00	0.07	0.29	0.44
Sagittaria graminea Michx.	1.00	1.23	0.60	2.34
Isoetid allies	4.41	4.86	4.94	5.88
Percent total coverage	9.3	24.9	25.4	26.0
Elatine minima (Nutt.) Fisch. and Meyer	0.01	0.01	0.02	0.03
Eleocharis acicularis (L.) R. and S.	—	0.34	0.47	0.75
Myriophyllum tenellum Bigel.	2.30	1.98	3.31	3.11
Scirpus subterminalis Torr.	0.60	0.14	0.05	0.28
Utricularia resupinata Greene	1.50	2.39	1.09	1.71
Floating-leafed plants	0.32	1.92	2.37	2.94
Percent total coverage	0.7	9.9	12.2	13.0
Brasenia schreberi Gmel.	0.01	0.51	0.29	0.9
Glyceria pallida (Torr.) Trin.	—	—	—	0.02
Nuphar luteum	0.20	0.62	0.27	0.84
Nymphaea odorata Ait.	—	0.04	0.14	0.17
Nymphoides cordata (Ell.) Fernald.	0.01	0.01	0.09	0.10
Sparganium fluctuans (Morong) Robinson	0.10	0.74	1.58	0.91
Caulescent canopy-formers	0	1.86	3.89	3.87
Percent total coverage	0.0	9.5	20.0	17.1
Potamogeton confervoides Reichenb.	—	0.01	—	0.06
Potamogeton epihydrus Raf.	—	1.85	3.89	3.81
Bladderworts, nonrooted	35.71	6.43	0.50	1.86
Percent total coverage	75.0	32.8	2.6	8.2
Utricularia geminiscapa Benj.	0.01	0.01	—	—
Utricularia purpurea Walt.	35.7	6.43	0.50	1.86
Mosses	0.3	0	0	0
Percent total coverage	0.6	0.0	0.0	0.0
Sphagnum sp.	0.30	—	—	—
Charids	—	0.05	0.07	0.24
Percent total coverage	0.0	0.3	0.4	1.1
Nitella flexilis	—	—	—	0.01
Nitella hyalina	—	0.05	0.07	0.23
Total percent coverage	47.62	19.59	19.46	22.61
Species richness	16	20	18	21
Shannon diversity (base 2)	1.45	3.07	2.92	3.52
Evenness	0.36	0.71	0.70	0.80

and evenness as

$$\{\Sigma[(p_i)\log_2(p_i)]\}/[\log_2(S)]$$

where p_i is the proportion of the total coverage represented by species i and S is species richness.

Results

Pronounced changes in macrophyte species diversity and community composition were apparent following lake and watershed limings (Table 1). Richness, diversity, and evenness increased following lake neutralization. Seven new species were observed during the 1989–91 surveys which were not reported during the preliming (1981) survey: *Eleocharis acicularis*, *Glyceria pallida*, *Nitella flexilis*, *Nitella hyalina*, *Nymphaea odorata*, and *Potamogeton epihydrus*. Two species that were observed in 1981 were not encountered in the postliming surveys: *Utricularia geminiscapa* and a *Sphagnum* sp. Overall, macrophyte coverage decreased by ~57%. The decrease in coverage was mostly due to the dieback of *U. purpurea* (from ~36% coverage to ~2% in 1990). The most successful of the immigrant species was

P. epihydrus which accounted for 17% of the total community coverage in 1991.

Percent coverage estimates of macrophyte species were tabulated according to plant growth forms (Table 1). The distinction among functional groups is made in the sense of traditional ideas of macrophyte zonation (Hutchinson 1975; Wetzel 1983) in order to describe the structural changes in the macrophyte community. Plants mostly found at depths less than 1 m, the isoetids and isoetid allies (species sympatric to the isoetids), did not increase in total coverage but did increase in their relative abundance due to the decline of *U. purpurea*. The floating-leafed plants/nymphaeids and the caulescent canopy-formers increased both in their total coverage and in their relative abundance. The most striking changes were observed among the nonrooted bladderworts which decreased in both total and relative abundance (*U. resupinata* was included with the isoetid allies due to its restriction to very shallow water and similar growth form).

Pronounced changes in the depth distribution of macrophytes were also observed after liming, relative to the 1981 survey (Fig. 2). Prior to liming, mixed isoetids and isoetid allies were abundant from the shoreline to 2 m. From 1 m to about 7 m the bladderwort *U. purpurea* dominated. Highest percent coverage was observed at 1–2 m where nearshore isoetids (and isoetid allies) overlapped with deeper beds of *U. purpurea* and at depths greater than 7 m where *U. purpurea* was abundant. After liming, the isoetids and isoetid allies were largely unchanged. Floating-leafed plants expanded and a floating-leafed zone from ~0.5 to 2 m was evident in many areas of the lake. From 1 to 3.5 m, pondweeds, almost entirely *P. epihydrus*, were prevalent. Percent coverage was reduced at depths greater than 1 m and very few plants grew at depths greater than 3 m. The reductions in coverage at the various depths were correlated with the reduction in light availability (Bukaveckas and Driscoll 1991).

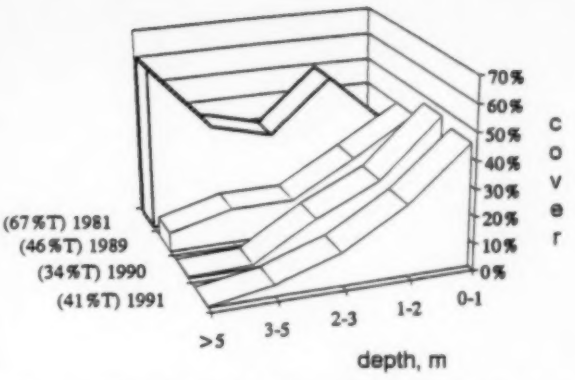

FIG. 2. Depth distribution of macrophyte percentage cover in Woods Lake, New York, percent transmission (% *T*) of subsurface PAR at 2 m (data from Bukaveckas and Driscoll 1991).

Discussion

Community Responses

Richness, diversity, and evenness increased following neutralization because of the new species that became established in the lake and the decline of the previously dominant *U. purpurea*. Other liming experiments have resulted in various responses. In Bowland Lake, Ontario, two species were replaced and richness was unchanged (Jackson et al. 1990). Immigration of *P. natans* and increased coverage of floating-leafed species were observed in two of four limed Swedish lakes (Eriksson et al. 1983). Other studies have not shown major increases in species such as we observed in Woods Lake.

The macrophyte community of Woods Lake appears to be in transition from that of a typical acidic Adirondack lake to that of a circumneutral Adirondack lake. A floating-leafed zone has become established in the nearshore areas. The spread of *P. epihydrus* and the decline of *U. purpurea* in the submersed plant zone indicate a shift in community structure that is more characteristic of circumneutral lakes.

The increased coverage of the nymphaeids and *P. epihydrus* suggests that competition for light may now be more important in determining community structure. Plant height is correlated with competitive ability in aquatic plants (Keddy and Shipley 1989). Nymphaeids and pondweeds are likely better competitors for light in comparison with relatively diminutive plants such as *Utricularia* sp. (Murphy et al. 1990). Throughout the posttreatment period, light attenuation was significantly higher (Fig. 1) (Bukaveckas and Driscoll 1991). In general, tall canopy-forming species are adapted for competition for light, while a lower growing carnivorous species such as *U. purpurea* is more likely adapted for stress tolerance (Grime 1979; Murphy et al. 1990) or competition for nutrients (Tilman 1982). The correlation between the expansion in coverage of plants that are adapted for competition for light while light availability was decreasing suggests that light has become relatively more limiting.

Prior to treatment, Woods Lake had the highest documented species richness of any lake in the Adirondack region with pH below 5.6 (Roberts et al. 1985; Jackson and Charles 1988). Therefore, it is somewhat surprising that a further increase in species richness was observed after liming. Weiher (1992) used an island biogeographic approach to model aquatic plant species richness in Adirondack lakes and reported positive correlations with lake surface area, pH, and connectedness. This species–area model predicts an increase of approximately two species per unit increase in pH. The net increase of four species may be interpreted as evidence supporting the importance of pH as a controlling variable because even this relatively species-rich lake showed net immigration upon lake neutralization. The net gain in species richness may not be a direct response to pH increase, but rather a response to greater variability in pH. The liming–reacidification cycles that have occurred may allow for the survival and persistence of species that prefer acid conditions *and* species that prefer circumneutral conditions.

Population Responses

Potamogeton epihydrus was the most successful immigrant to Woods Lake. It has become the most abundant species (Table 1). It is a common species in Adirondack lakes where the pH is greater than 5.3 (Roberts et al. 1985; Jackson and Charles 1988). In this sense, it may be called a moderately acid-tolerant species although it is not found in the most acidic lakes. In New England, it was found in 48% of the locations surveyed and was found in lakes with alkalinities ranging from 48 to 3234 $\mu eq \cdot L^{-1}$ (Hellquist 1980).

Although it is most often found at locations with low to moderate alkalinity, it may also be found at higher alkalinities. This apparent niche breadth in terms of alkalinity has likely made it successful in the fluctuating alkalinity of Woods Lake. The immigration of *P. epihydrus* provides a new physical habitat in Woods Lake. Prior to treatment, there were no pondweeds or any caulescent macrophytes capable of producing a complex plant canopy within the water column. The dense beds of *P. epihydrus* that are now spreading provide substrate for invertebrates and habitat for young-of-the-year fish. The extirpation of *Sphagnum* was not unexpected, since most *Sphagnum* species cannot survive conditions where pH and calcium are high (Clymo 1973). *Sphagnum* is rarely found in lakes with pH above 5.0 (Roberts et al. 1985; Jackson and Charles 1988).

The reduction in *U. purpurea* was a major cause of the observed increases in diversity and evenness. The die-back of this species has been attributed to reductions in light penetration during the postliming period (Bukaveckas 1989). Photosynthesis in *U. purpurea* has been shown to be saturated at 35% incident radiation (Moeller 1980), and therefore, growth should be negatively affected at depths where light availability was reduced to below 35% (>2–3 m depth). Furthermore, *U. purpurea* is an obligate CO_2 user (Moeller 1978), and the addition of carbonate materials changed the predominant form of carbon from dissolved CO_2 to HCO_3^-. Other populations of *U. purpurea* do well in lakes that exhibit conditions similar to those now found in Woods Lake. In Deer Pond, New York (pH 6.9), *U. purpurea* is the most abundant species (Roberts et al. 1985) where it forms dense beds at depths where light is 2.5% of subsurface photosynthetically active radiation (PAR) (personal observation).

The Woods Lake macrophyte community responded to liming with increased richness and diversity. The community is apparently in a transitional state from a typical acidic community to a typical circumneutral community. The floating-leafed zone has expanded and the submersed plant zone has changed from dominance by *U. purpurea* to dominance by *P. epihydrus*. Some population-level responses to neutralization were not consistent with the known physiological ecology or biogeographical distribution of species, and therefore, other factors such as local adaptation may contribute to specific responses.

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Relationships between Suspended Particulate Matter and Sinking Flux along a Trophic Gradient and Implications for the Fate of Planktonic Primary Production

Stephen B. Baines[1]

Institute of Ecosystem Studies, The New York Botanical Garden, Box AB, Millbrook, NY 12545-0129, USA
and
Yale University, Department of Biology, Osborne Memorial Laboratory, 195 Prospect St., New Haven, CT 06511, USA

and Michael L. Pace

Institue of Ecosystem Studies, The New York Botanical Garden, Box AB, Millbrook, NY 12545-0129, USA

Baines, S.B., and M.L. Pace. 1994. Relationships between suspended particulate matter and sinking flux along a trophic gradient and implications for the fate of phytoplankton production. Can. J. Fish. Aquat. Sci. 51: 25–36.

We measured water column variables and the sinking flux of C, N, P and pigments in 15 lakes which varied in algal biomass to determine (1) the relationship between sinking flux and suspended particulate concentrations, (2) if sinking rates of particles changed as a function of trophic status, and (3) the importance of sinking as a fate for phytoplankton production along a trophic gradient. Sinking flux was well predicted by metalimnetic algal pigment concentrations (chlorophyll + phaeopigments) and epilimnetic C:N ratios (R^2 = 83–97%). Sinking rates of algal pigments were not significantly higher in lakes with higher chlorophyll concentrations. Predictions based on observed C sinking fluxes, water column chlorophyll, and an empirical relationship between primary production and chlorophyll concur with published observations in suggesting a slight negative relationship between production and the ratio of sinking flux to production. Our results challenge the notion that plankton communities in oligotrophic lakes are more efficient than those in eutrophic lakes in the retention of nutrients within the water column.

Nous avons mesuré des variables de la colonne d'eau et l'enfoncement du C, du N, du P et des pigments dans 15 lacs à biomasse algale variable afin d'établir 1) le rapport entre l'enfoncement et les concentrations de particules en suspension, 2) si la vitesse verticale des particules changeait comme fonction de l'état trophique et 3) l'importance de l'enfoncement comme devenir de la production phytoplanctonique le long d'un gradient trophique. Le flux d'enfoncement a été bien prédit par les concentrations de pigment d'algue métalimnétique (chlorophylle + phaeopigments) et des rapports C:N (R^2 = 83–97 %) dans l'épilimnion. La vitesse d'enfoncement des pigments des algues n'étaient pas significativement plus élevée dans les lacs à teneur plus élevée en chlorophylle. Des prévisions fondées sur l'enfoncement observé du C, de la chlorophylle dans la colonne d'eau et d'un rapport empirique entre la production primaire et la chlorophylle correspondent aux observations publiées en proposant un rapport légèrement négatif entre la production et le rapport entre l'enfoncement et la production. Nos résultats remettent en question la notion selon laquelle les communautés planctoniques des lacs oligotrophes retiennent plus efficacement les substances nutritives dans la colonne d'eau que celles des lacs eutrophes.

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The sinking of organic particles into the hypolimnion is one of the most important fates of phytoplankton production in stratified lakes. Estimates of the fraction of annual phytoplankton production lost to sinking, as opposed to respiration and outflow, can vary from 10 to 50% (Forsberg 1985; Stabel 1985; Bloesch and Uehlinger 1990). The magnitude of the sinking flux relative to the other fates will determine, in part, the response of a lake to changes in nutrient loads, pollutant inputs, and food web structure (Sigg et al. 1987; Ahlgren et al. 1988; Carpenter et al. 1988; Landers and Mitchell 1988). Therefore, models that successfully account for variability in sinking flux among lakes could enhance the prediction of lake responses to environmental perturbations.

Unfortunately, such models do not exist. While patterns of sinking export have been widely examined in marine pelagic ecosystems (Suess 1980; Pace et al. 1987; Wassman 1990), most limnological research on sinking fluxes has focused on single lakes. Experimental manipulations, budgeting studies, and mechanistic models have indicated that a number of variables affect sinking fluxes in lakes. Physical variables, such as particle number, mass, shape, and density, as well as ambient liquid viscosity and turbulence (Hutchinson 1957), control settling flux directly. These first-order variables are, in turn, influenced by water chemistry (Weilenmann et al. 1989), plankton community structure and trophic interactions (Uehlinger and Bloesch 1987; Carpenter et al. 1988; Bloesch

[1]Present address: Department of Biology, McGill University, 1205 Avenue Docteur Penfield, Montreal, QB H3A 1B1, Canada.

TABLE 1. Data summary. Trap depth and concentrations are means for each sampling date in 1989. Concentrations averaged over whole water column. ND = no data.

Lake	Area (h)	Date	Trap depth (m)	Suspended particulate matter			Sinking fluxes			
				Chlorophyll ($mg \cdot m^{-3}$)	C ($mg \cdot m^{-3}$)	N ($mg \cdot m^{-3}$)	Pigments ($mg \cdot m^{-2} \cdot d^{-1}$)	C ($mg \cdot m^{-2} \cdot d^{-1}$)	N ($mg \cdot m^{-2} \cdot d^{-1}$)	P ($mg \cdot m^{-2} \cdot d^{-1}$)
Awosting, N.Y.	37	27 June	9.0	0.53	375	50.9	0.19	53	6.5	0.77
Bull Pond, N.Y.	12	19 June	6.0	4.57	823	127.1	2.82	220	28.7	3.04
Bull Pond, N.Y.		24 July	6.0	5.59	837	112.2	2.28	158	20.7	3.35
Bull Pond, N.Y.		16 Oct.	9.0	4.89	652	96.8	0.88	94	15.5	2.15
East Twin, Conn.	223	11 July	10.0	5.92	1073	118.6	2.72	260	42.2	5.05
East Twin, Conn.		8 Aug.	9.0	6.31	1157	156.7	2.14	305	39.6	3.99
Gilead, N.Y.	49	18 July	9.0	9.53	899	129.1	3.00	224	36.8	7.34
Gilead, N.Y.		30 Aug.	9.0	11.40	1071	193.4	2.23	187	28.8	ND
Gilead, N.Y.		19 Sept.	10.5	12.85	1068	183.1	2.05	161	25.7	3.55
Giles, Pa.	47	30 May	9.5	0.45	431	54.9	0.18	77	8.1	1.42
Giles, Pa.		26 June	9.0	0.88	296	41.7	1.72	109	11.0	1.94
Giles, Pa.		11 Sept.	16.5	3.58	555	82.4	2.08	86	13.5	2.20
Iron Mine Pond, N.Y.	2	11 July	7.5	2.98	716	86.6	0.77	160	17.1	2.98
Iron Mine Pond, N.Y.		6 Sept.	10.5	4.35	886	112.4	1.09	159	21.1	5.25
Iron Mine Pond, N.Y.		27 Sept.	10.5	4.91	772	120.7	1.25	157	22.4	2.93
Lacawac, Pa.	21	31 May	6.0	7.87	931	130.6	1.38	109	13.3	2.32
Lacawac, Pa.		26 June	6.0	5.11	844	106.9	3.60	193	27.2	3.20
Lacawac, Pa.		11 Sept.	5.0	3.37	794	101.2	3.13	408	63.2	8.60
Log Tavern, Pa.		27 June	6.0	1.99	404	54.7	0.76	125	16.3	3.97
Log Tavern, Pa.		12 Sept.	7.5	1.58	431	59.3	0.69	67	11.0	2.29
Minnewaska, N.Y.		17 July	9.0	0.68	333	49.9	0.27	33	3.1	0.91
Minnewaska, N.Y.		28 Aug.	12.0	0.70	512	85.5	0.16	26	3.9	0.88
Minnewaska, N.Y.		21 Sept.	15.0	1.33	420	59.3	0.51	64	7.3	0.75
Popolopen, N.Y.	60	22 May	4.5	2.57	1039	120.3	0.53	142	15.1	2.35
Popolopen, N.Y.		18 June	7.0	3.38	750	116.3	2.87	182	24.8	3.67
Popolopen, N.Y.		24 July	6.0	7.80	740	118.9	5.52	281	44.4	8.40
Round Pond, N.Y.	5	22 May	3.0	4.21	1164	151.0	0.27	88	8.6	1.29
Round Pond, N.Y.		19 June	6.0	2.31	871	140.6	0.66	120	20.8	3.37
Tyrell, N.Y.	18	4 June	4.5	4.24	1383	159.7	5.74	334	47.3	5.54
Tyrell, N.Y.		18 July	5.0	33.00	2518	380.7	4.90	332	42.3	4.09
Upton, N.Y.	13	23 May	3.0	5.84	1890	215.5	2.05	325	39.9	5.61
Upton, N.Y.		2 Aug.	6.0	18.46	2164	293.0	6.38	459	55.6	8.70
Upton, N.Y.		20 Sept.	6.0	9.15	869	144.2	4.02	307	50.2	6.97
Waynewood, Pa.	27	30 May	6.0	2.84	1066	101.5	4.13	324	34.0	6.84
Waynewood, Pa.		28 June	4.5	16.72	1567	220.2	7.09	362	45.8	8.27
Waynewood, Pa.		12 Sept.	3.0	14.69	1508	216.0	2.91	232	41.1	4.80
Wononscopomuc, Conn.	143	10 July	7.5	3.23	721	74.5	1.79	178	24.7	3.84
Wononscopomuc, Conn.		7 Aug.	10.5	4.43	788	101.2	3.08	425	52.6	ND
Wononscopomuc, Conn.		5 Sept.	12.0	2.99	1138	172.0	0.95	141	22.1	2.99

and Burgi 1989), and the physiological state of the plankton (Walsby and Reynolds 1979). In combination, these effects result in a 10- to 20-fold range in mean sinking rates for communities of suspended particles (Bloesch and Sturm 1985). Unfortunately, lack of a standardization in sediment trap design and technique has thwarted broad comparisons of sinking fluxes among lakes (Bloesch and Burns 1980; Gardner 1980a, 1980b; Blomquist and Håkanson 1981). As a result, the relative importance of the various factors determining sinking fluxes remains largely unknown.

The fraction of planktonic primary production that sinks from the euphotic or trophogenic zone, which we will refer to as the "export ratio", is expected to be higher in more productive aquatic systems (Reynolds 1984; Harris 1986). This pattern is supported by the consensus of empirical models relating the sinking flux of organic C to primary production in marine ecosystems (summarized in Bishop 1989). A similar expectation exists for lakes (Reynolds 1984), since the phytoplankton of eutrophic lakes tend to be dominated by large forms (Watson and Kalff 1981) with high potential sinking rates (Walsby and Reynolds 1979) and low vulnerability to herbivory (Burns 1968) whereas oligotrophic lakes are dominated by smaller phytoplankters (Watson and Kalff 1981) that sink less readily and are grazed easily (Reynolds 1984). Other possible explanations for higher export ratios in more productive systems are increased aggregation rates resulting from more frequent particle collisions at higher particle densities (Hahn and Stumm 1970), and greater decoupling of phytoplankton growth and remineralization where phytoplankton production is more dynamic (Sommer et al. 1986). Relationships that suggest that the fraction of primary production lost to heterotrophic respiration declines with lake productivity imply a positive relationship between the export ratio and planktonic primary production (Cole et al. 1988). However, countering the expected pattern are tendencies for both measured sinking flux and benthic respiration to account for less primary production in more productive ecosystems (Hargrave 1973; Stabel 1985).

In this study, we examine the relationship of several chemical constituents of suspended particulate matter with the sinking fluxes of these constituents into the hypolimnia of lakes spanning a trophic gradient. The influence of depth and temperature on sinking fluxes is also evaluated. In addition, we test whether sinking rates of particulate matter increase with total algal biomass. Finally, we determine whether a positive relationship between primary production and the fraction of that production lost to sinking is consistent with regression models developed here and data from the literature.

Methods

Study Sites

Fifteen lakes in New York, Pennsylvania, and Connecticut were selected for study (Table 1). Selection criteria included relatively long hydrological residence times (>1 yr during stratification), well-developed thermal stratification, limited littoral macrophyte development, and sufficient depth to allow sediment traps to be placed at least 2 m above the bottom. These criteria insured that the patterns we detected resulted primarily from water column processes and not the import of allochthonous or littoral material or the resuspension of sediments. Lakes were sampled two to three times over the course of the stratified season. We sampled during stratification (late May to early October), since resuspension was limited at this time.

Sediment Trap Design

Sediment traps were constructed according to the recommendations of Bloesch and Burns (1980) and Blomquist and Håkanson (1981) with some modifications. Each sediment trap consisted of a hollow polyvinylchloride cylinder (internal diameter = 7.50 cm) open at the top and with a polyethylene funnel at the bottom. The height of the cylinder was five times the internal diameter. This ratio was adequate to maintain a depositional environment within the traps under the low turbulence conditions of the lower metalimnion (Gardner 1980a; Blomquist and Kofoed 1981). A plastic tube was attached to the funnel stem to drain samples directly from the bottom of the cylinder.

Four cylinders were bound with elastic cords against the inside corners of a plastic milk crate ($1 \times 0.5 \times 0.5$ m). Styrofoam strapped across the tops of the crates made the crates buoyant. Stabilizing ropes connected all four corners of each crate bottom to a ring which hung 1 m below the tops of the cylinders. An anchor was attached to this ring by a rope, the length of which was determined by the depth of the site and the depth at which the tops of the cylinders were to rest. This system allowed for accurate placement of the traps and insured that the cylinders were never tilted off the vertical. The traps were filled with deionized water, and 500 mL of saline solution (0.75% NaCl) was siphoned into the bottoms of the cylinders before deployment to provide a density barrier to turbulent eddies.

Saline solutions may enhance flux estimates by causing animals to expel ingested material (Petersen and Dam 1991). Assuming a *Daphnia pulex* gut capacity of 3 ng chlorophyll (Christoffersen 1991), complete gut evacuation upon entering the traps, and a carbon to chlorophyll ratio of 100:1 for defecated material, we find that a concentration of 300 *Daphnia*·L^{-1} in the traps would bias our lowest carbon flux estimates by 1%. Since *D. pulex* is among the largest of freshwater macrozooplankton, even greater densities of other taxa would be needed before our measurements were affected. We never observed cladoceran or copepod densities of this order of magnitude.

Determination of Trap and Sampling Depths

Traps were positioned at the lower boundary of the metalimnion according to vertical temperature profiles. Just prior to deployment, temperature and dissolved oxygen were measured over 1-m depth intervals using a YSI model 57 oxygen meter. The tops of the trap cylinders were positioned at the top of the hypolimnion (1.5 times the depth of maximum temperature change). Trapping of particles resuspended from the benthos or of artificially precipitated from anaerobic hypolimnetic waters was reduced by constraining trap depth to be at least 2 m from the lake bottom and 1 m above the 1 mg O_2·L^{-1} oxycline. The traps were deployed for 1–4 d (average = 3 d) except for Lake Minnewaska in September when the deployment period was 8 d. The short deployment period was intended to reduce contamination by zooplankton and losses of C due to res-

piration of settled material (Bloesch and Burns 1980). No preservatives were used in the traps.

The water column above the traps was divided into three sampling strata, hereafter referred to as the epilimnion, the metalimnion, and the trap depth. The bottom of the epilimnion was defined as the shallowest depth at which the change in temperature exceeded $2°C \cdot m^{-1}$. The metalimnion spanned the interval between the bottom of the epilimnion and 1.5 times the depth of maximum temperature change. The trap depth was the 1-m layer directly above the traps.

Sampling and Analyses

Water column samples were taken using a 3-L Van Dorn bottle at the time of trap deployment. Depth integrated samples were obtained for the epilimnion and the metalimnion by pooling bottle casts taken from the top, middle, and bottom of each layer. Duplicate pooled samples of the metalimnion and epilimnion were taken. The trap depth was sampled without replication by pooling three bottle casts. Triplicate samples of settled material were collected by draining 500 mL from each of three trap cylinders into separate plastic bottles.

Six subsamples were taken from each pooled water column sample and each trap cylinder sample and passed through Whatman GF/F filters. Cylinder samples were well shaken before a subsample was poured into a graduated cylinder and then rinsed into the filtration tower. Visible zooplankton were removed from the filters using forceps and a 15× magnification hand lens. Rotifers and nauplii could not be removed because of their small size. The total biovolume of these organisms was estimated using geometric formulae and regressions (McCauley 1984) and was found to contribute <10% to the measured C flux. Filters to be analyzed for pigments were frozen at −4°C and analyzed within a month of collection. Filters to be analyzed for C, N, and P were dried for over 24 h at 60°C and then stored in a desiccator.

One filter from each sample was analyzed for total C and N using a Carlo-Erba C-N-S elemental analyzer. Both organic and inorganic forms of C are oxidized at the combustion temperature used (1000°C). Typically, one filter from each pooled water column sample and each trap cylinder was analyzed.

P was measured in triplicate for each pooled water column sample and trap cylinder. Filters to be analyzed for P were first ashed at 500°C for 5 h and then hydrolyzed with a 1 N solution of H_2SO_4 in an autoclave at approximately 103 kPa and 121°C for 1 h (Solarzano and Sharp 1980). Orthophosphate concentration in the resulting sample was measured spectrophotometrically using the ascorbic acid modification of the standard molybdate reduction method (American Public Health Association 1989). High background concentrations of P associated with the glass fiber filters interfered with our estimates of suspended particulate P. These data have been excluded from our analyses. Since there was a greater amount of material collected on filters from the sediment traps, this interference was less of a problem for sinking flux estimates. We only include the P fluxes to determine if they follow patterns similar to those for C and N sinking fluxes.

Pigment concentrations were measured using a Turner fluorometer after extraction of the filters in basic methanol (1 L of 100% MeOH + 2 mL of 1 N NaOH) at room temperature (Holm-Hansen and Riemann 1978). After the initial fluorescence reading, 4 mL of extract was acidified with 40 μL of 0.03 N HCl. The reduction in fluorescence due to acidification was measured. This value was used to correct the chlorophyll measurements for phaeopigments. At least two filters were analyzed from each pooled water column sample and each trap cylinder. Since chlorophyll is transformed into phaeopigments in sediment traps over time (Leavitt and Carpenter 1990), we summed phaeopigments and corrected chlorophyll to produce an estimate of total pigments. For the sake of simplicity, we shall refer to the corrected chlorophyll estimates as simply "chlorophyll" whereas the sum of corrected chlorophyll and phaeopigments will be called "pigments".

The sinking flux of a material x (S_x, milligrams per square metre per day) was calculated according to

$$(1)\quad S_x = 24 \cdot [X] \cdot V \cdot A^{-1} \cdot D^{-1}$$

assuming a collection volume (V, cubic metres) of 0.5 L and a collection surface area (A) equal to the area of the cylinder mouth (=0.00456 m^2) and where D is the deployment period in hours and $[X]$ (milligrams per cubic metre) is the measured concentration of either pigments, C, N, or P in the 500-mL sample volume. The coefficient of variation of sinking flux estimates among cylinders averaged approximately 10% for all constituents. Average sinking rate of a material x (v_x, metres per day) was calculated according to

$$(2)\quad v_x = S_x/[X]$$

for C, N, and pigments (Hargrave and Burns 1979). Metalimnetic concentration of suspended C, N, and pigments was used in equation 2, since the traps were always positioned immediately below this stratum.

Export Ratio Estimation and Validation

The export ratio (E) can be defined in terms of the sinking flux of C from the euphotic zone (S_C, milligrams C per square metre per day), the volumetric primary production within the euphotic zone (PP, milligrams C per cubic metre per day), and the depth of the euphotic zone (Z_{eu})

$$(3)\quad E = S_C/(PP \cdot Z_{eu}).$$

To determine if the export ratio increased with algal biomass, we predicted the export ratio for our lakes using equation 3. Lake mean S_C was estimated directly. The euphotic zone depth was defined as the depth at which ambient light flux reached 1% of that just below the lake surface. It was determined either directly with a light meter or indirectly by assuming that the ambient light at the Secchi depth was 15% of the surface value ($2.4 \times Z_{Secchi} = Z_{eu}$) (Beeton 1957). In the case of Lake Minnewaska, the Secchi disc depth was determined from epilimnetic chlorophyll concentrations using the equation of Carlson (1977). Light meter and Secchi disc data for Lakes Lacawac, Giles, and Waynewood were provided by the Poconos Lakes Comparative Lake Program (Dr. Robert Moeller, Department of Biology, Lehigh University, Bethlehem, Pa.). Primary productivity was determined from lake means of water column average chlorophyll using a regression based on literature data (described in General Implications below).

Our export ratio relationship was compared with a relationship based on direct observations from the literature. We cited studies that employed criteria for trap design and

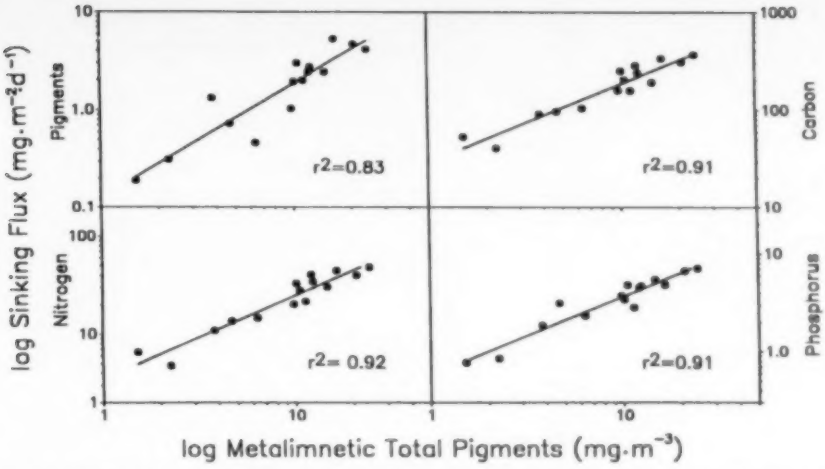

FIG. 1. Sinking fluxes of pigments, C, N, and P versus metalimnetic pigment concentration. The solid lines represent regressions.

placement that were similar to our own. Sinking flux estimates from Mirror Lake based on conical traps were multiplied by 1.3 (Caraco et al. 1992).

Statistical Treatment

For both the individual observations and the lake means, we developed linear regression models for each flux we measured. Unless otherwise stated, all variables required log(10) transformation to stabilize the variance. All reported R^2 values are adjusted for the number of observations and parameters to facilitate comparisons. Analyses were performed in SAS (version 6.03).

The best combination of predictor variables was determined using a forward stepwise selection procedure (Draper and Smith 1981). The thickness and temperature of each water stratum, the depth of the water column above the traps, and all concentrations, areal standing stocks, and material ratios in each stratum were considered as potential predictors. Exit and entry alpha levels for the stepwise procedure were low (0.01) because the high number of potential predictors inflated the probability of including spurious predictor variables. Several mechanistically reasonable combinations of variables that did not appear in the stepwise procedure were directly regressed against flux estimates to be certain that their exclusion was appropriate. We used partial sums of squares to determine if the predictors selected in the stepwise procedure explained a significant amount of variance in excess of other closely correlated predictor variables (Draper and Smith 1981). Partial R^2 and F values were calculated by dividing the partial sum of squares by the total sum of squares and the residual sum of squares, respectively.

Sinking rates of lake mean and unaveraged C, N, and pigments were regressed on water column averaged chlorophyll concentrations to determine if sinking rates increased with algal biomass. The a priori hypothesis that the regression slopes > 1 was subjected to a one-tailed t-test. We adopted a low critical p-value of 0.01 to control for Type I error, since six separate regressions were tested.

Results and Discussion

Composition of Suspended Particles and Settling Material

Suspended concentrations and fluxes of particulate matter varied widely, indicating a gradient in lake trophic status (Table 1). Lake means of average water column concentrations of particulate C, particulate N, and chlorophyll varied from 375 to 1950, from 51 to 270, and from 0.53 to 18.6 mg·m^{-3}, respectively. Fluxes ranged from 40.9 to 364, from 4.75 to 48.6, and from 0.19 to 5.32 mg·m^{-2}·d^{-1} for C, N, and pigments, respectively.

There was a high degree of correlation among the chemical parameters. Particulate C and N concentrations were highly correlated in all strata in the water column (r = 0.92–0.97) and in settled material (r = 0.96). Particulate C and N were less well correlated with pigment concentrations in the water column (r = 0.68–0.92) and in settled material (r = 0.81–0.82). In every case, particulate N was better correlated with pigments than was particulate C. The correlation of particulate C and N with pigments was higher in the epilimnion (r = 0.85, 0.92) than in the metalimnion (r = 0.80, 0.85) and at the trap depth (r = 0.68, 0.71).

C:pigment and N:pigment ratios were negatively correlated with pigment concentrations ($p < 0.0001$). Particulate C:N ratios, however, did not change significantly along the trophic gradient ($p > 0.10$). Therefore, changes in the relative contribution of allochthonous and precipitated C, both of which are characterized by high C:N as well as high C:pigment and N:pigment, are probably not responsible for the shift in the C:pigment and N:pigment ratios along the trophic gradient. Physiological adaptation of phytoplankton to different light and nutrient regimes (Harris 1978) and changes in the relative contribution of bacteria to seston (Pridmore et al. 1989) are more probable explanations.

Prediction of Sinking Fluxes

Metalimnetic algal pigment concentration was the best predictor for every sinking flux (Table 2; Fig. 1). This variable explained between 59 and 67% of the variances in the

TABLE 2. Best fit regressions for sinking fluxes. Pig_{Meta} and $C:N_{Epi}$ refer to metalimnetic pigment fluxes and epilimnetic C:N ratios, respectively.

Fluxing material	Model	n	p	R^2
	Unaveraged data			
log pigments	$= -0.77 + 1.02 \log Pig_{Meta}$	39	<0.0001	0.66
log C	$= 0.04 + 0.60 \log Pig_{Meta} + 1.87 \log C:N_{Epi}$	39	<0.0001	0.76
log N	$= -0.49 + 0.69 \log Pig_{Meta} + 1.38 \log C:N_{Epi}$	39	<0.0001	0.73
log P	$= -1.13 + 0.59 \log Pig_{Meta} + 1.28 \log C:N_{Epi}$	37	<0.0001	0.66
	Lake means			
log pigments	$= -0.90 + 1.16 \log Pig_{Meta}$	15	<0.0001	0.83
log C	$= -0.23 + 0.62 \log Pig_{Meta} + 2.16 \log C:N_{Epi}$	15	<0.0001	0.97
log N	$= -0.95 + 0.70 \log Pig_{Meta} + 1.90 \log C:N_{Epi}$	15	<0.0001	0.95
log P	$= -0.24 + 0.81 \log Pig_{Meta}$	15	<0.0001	0.91

TABLE 3. Percentages of variance in unaveraged flux estimates that are exclusively related to metalimnetic pigment concentrations and several correlated variables. Three models containing three predictors apiece were regressed on each of the four fluxes measured. All models include metalimnetic pigment concentrations (Pig_{Meta}) as a predictor. Model 1 also includes pigment concentrations from the epilimnion (Pig_{Epi}) and trap depth (Pig_{TZ}); Model 2, metalimnetic concentrations of particulate C (PC_{Meta}) and N (PN_{Meta}); Model 3, standing stocks of pigments integrated over the entire water column (Areal-Pig_{Tot}) and over the metalimnion (Areal-Pig_{Meta}). See text for details of calculation. Legend for p-values: *$0.05 > p > 0.01$, **$0.01 > p > 0.001$, ***$p < 0.001$.

	Predictors								
	Model 1			Model 2			Model 3		
Flux	log Pig_{Epi}	log Pig_{Met}	log Pig_{TZ}	log PC_{Met}	log PC_{Met}	log PN_{Met}	log Pig_{Met}	log Areal-Pig_{Met}	log Areal-Pig_{tot}
log pigment	1	11***	1	35***	0	2	14***	0	0
log C	0	4*	0	15***	5*	3	25***	0	1
log N	0	3	0	18***	2	1	23***	1	0
log P	0	9**	1	21**	2	2	23***	0	1

unaveraged sinking fluxes and from 83 to 92% of the variances in the lake mean fluxes. Chlorophyll was highly correlated with total pigments ($p = 0.98$, unaveraged data) and the regression results were similar when either was used to predict sinking fluxes. To stay consistent with the use of total pigments in the flux estimates, only analyses using total pigment concentrations are discussed further.

Other measures of suspended particulate matter are closely correlated with metalimnetic pigment concentration and consequently will possess similar power to predict fluxes. To verify that metalimnetic pigment concentration was the best predictor in a statistical sense, we regressed three different sets of variables on each of the measured fluxes and calculated the partial sums of squares and partial r^2's associated with each predictor. All three sets included metalimnetic pigment concentration as a predictor. Model 1 also included pigment concentrations in the two other strata. Model 2 contained metalimnetic particulate C and particulate N concentrations. Model 3 included the areal pigment standing crops integrated over just the metalimnion and over the entire water column above the traps.

Partial sums of squares indicate that metalimnetic pigment concentration almost always explained a significant fraction of the variance in sinking fluxes exclusive of the other predictors (Table 3). Metalimnetic concentrations of particulate C and particulate N and areal standing stocks of pigments were clearly inferior predictors (Table 3, Models 2 and 3). The comparison of the predictive ability of pigment concentrations from three strata was somewhat less conclusive (Table 3, Model 1). Metalimnetic pigment concentrations could explain a significant amount of the variance in pigment flux ($p = 0.0012$), P flux ($p = 0.0096$), and C flux ($p = 0.048$) independently of pigment concentrations in the epilimnion and at the trap depth. In contrast, N flux was not uniquely related to metalimnetic pigment concentrations ($p = 0.08$). In only one instance was there a weakly significant effect of another variable on settling flux independent of metalimnetic pigment concentration (i.e., metalimnetic particulate C concentrations in Model 2).

Epilimnetic particulate C:N was also positively related to the fluxes of C, N, and P (Table 3; Fig. 2), accounting for an additional 15, 7, and 7% of the total variances, respectively, based on the unaveraged data. When lake means were considered, epilimnetic particulate C:N explained an additional 6% of the total variance in C fluxes and 4% in N and P fluxes. Pigment fluxes were unrelated to particulate C:N. Autocorrelation is not the basis of the relationship between particulate C:N and flux, since the coefficient is positive even for N flux. Since we included both particulate C and particulate N concentrations as potential predictors, we also know that particulate C:N is not acting as a surrogate for these variables in the model (Prairie 1990).

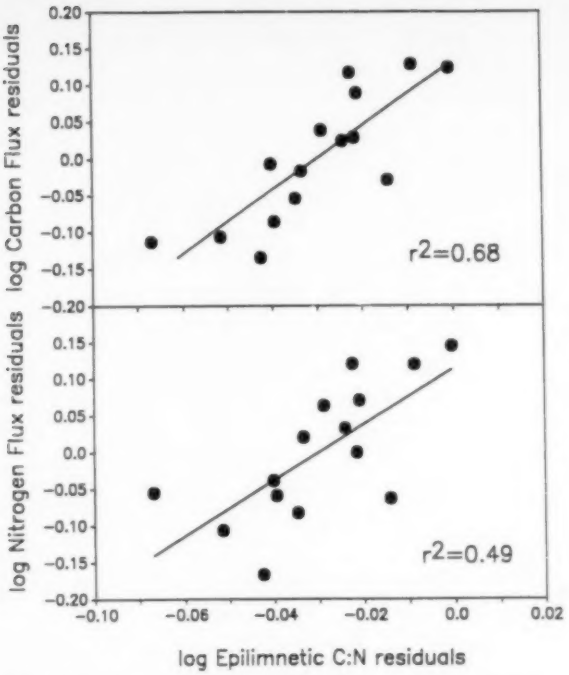

FIG. 2. Plot of residuals from the log–log regressions of C sinking flux, N sinking flux, and epilimnetic C:N ratio on metalimnetic pigment concentration. The solid lines represent the regressions of the residuals.

Using linear regressions, neither temperature nor any measure of strata or water column thickness entered as a significant predictor. These variables could not explain a significant amount of the variance ($p > 0.10$) when included directly in a model which also included metalimnetic pigments. The results were similar for lake means and unaveraged data and for log-transformed and untransformed data.

Potential Sources of Settled Particles

The large percentage of variance explained by pigment concentrations suggests that the sinking fluxes in the lakes we sampled were dominated by material derived from phytoplankton. Observed particulate C:N ratios are consistent with this interpretation. Values from settled and suspended material ranged from 5.4:1 to 11:1 by weight. These values are within the range typically exhibited by communities of phytoplankton (Healey and Hendzel 1980). The observed ratios are lower than those expected for terrestrial plant material (50:1, Hutchinson 1957), humic material from soils (24:1, Gosz et al. 1976), and littoral macrophyte material (15:1, Likens 1985). Qualitative inspection of the trap material revealed that recognizable allochthonous organic particles and calcite crystals were a small proportion of settled material. Microscopy also revealed obvious differences among samples. The particle volume consisted mostly of living cells in some samples and detritus in others.

The exact contribution of zooplankton fecal material to sinking fluxes was impossible to determine. Recognizeable fecal pellets were rarely encountered. Phaeopigments measured with fluorometry may be produced in a number of ways besides zooplankton herbivory (Daley 1973; Daley and Brown 1973; Carpenter et al. 1986) and may have been produced after the settled material entered the traps.

TABLE 4. C:pigment, N:pigment, and C:N ratios in suspended and settled material. Ratios from water column were compared pairwise to flux ratios using a sign rank test. Legend for p-values: *$0.05 > p > 0.01$, **$0.01 > p > 0.001$, ***$p < 0.001$.

	C:pigment	N:pigment	C:N
Epilimnion	186***	27***	7.2
Metalimnion	121	16	7.3
Trap depth	108*	15*	7.2
Flux	131	17	7.6

Two lines of evidence suggest that phytoplankton living in the epilimnion at the time of trap deployment contributed little to the measured sinking fluxes. First, epilimnetic pigment concentration is not uniquely related to the flux of any material (Table 3, Model 1). Second, a pairwise sign rank test on the unaveraged data revealed that C:pigment ratios of the settled material differed significantly from those of epilimnetic particles ($p < 0.0001$), but were similar to those of suspended particles in the metalimnion (Table 4). The same trend was apparent for the C:N ratios, but none of the differences between strata was significant. Our analyses suggest that sinking fluxes varied according to the distribution of phytoplankton biomass with depth in the water column. Processes that affect this distribution, such as defecation by migrating zooplankton, the sinking of defecated material or algal cells into the metalimnion, and production of algal cells within the metalimnion, may thus influence the fate of primary production.

The positive relationship of particulate C:N with C and N fluxes may indicate the precipitation and downward transport of calcite crystals or colloids (Stabel 1986). Such particles are important components of sinking flux in hard-water lakes when the consumption of CO_2 by algae causes pH to increase to the point where $CaCO_3$ is supersaturated (White and Wetzel 1975; Stabel 1985). While calcite crystals were not observed in large numbers in any of the trap samples, calcite was chronically supersaturated in Lake Wonunscopomuc and East Twin Lake. Carbonate crusts were also evident on littoral macrophytes in Upton Lake. It is possible that calcite contributed to the C sinking flux in these three lakes. However, removing these lakes from the data set resulted in coefficients for epilimnetic particulate C:N of 1.82 ($p = 0.003$) and 2.04 ($p = 0.0075$) for the regressions based on the unaveraged data and means, respectively. These coefficients are similar to those obtained for particulate C:N when the data from Wonunscopomuc, East Twin, and Upton lakes are included in the analysis. We conclude that calcite deposition is not causing the relationship between epilimnetic particulate C:N and C sinking flux.

The positive relationship between particulate C:N ratios and fluxes of C and N may reflect a secondary contribution by allochthonous or littoral macrophyte material to sinking fluxes. Although not abundant, pollen grains, trichomes, and other plant detritus were present in suspended and settled material. Rapid sinking of these detrital particles could explain why particulate C:N ratios would be moderately related to C and N sinking fluxes despite the relatively low C:N ratios observed in the study lakes. If we substitute the

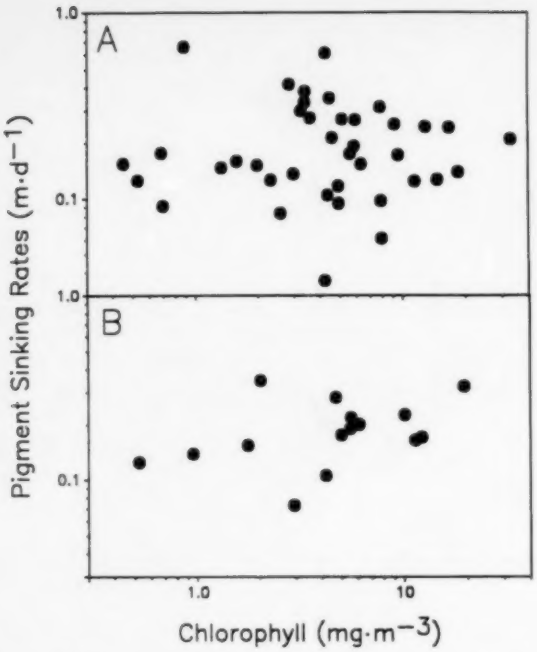

FIG. 3. Sinking rates of total pigments (chlorophyll + phaeopigments) as a function of chlorophyll concentration averaged over the water column for (A) unaveraged data and (B) lake means.

Redfield C:N ratio (6.1:1 by weight) into the best fit regression for C and N flux in Table 2, the predicted fluxes average 30% less than the fluxes actually measured. This difference may roughly indicate the average contribution of allochthonous material to C flux in our data.

Sinking Rates and Algal Biomass

Calculated sinking rates of C, N, and pigments, while they varied widely among sampling dates and lakes, averaged between 0.21 and 0.22 $m \cdot d^{-1}$ and did not differ systematically from one another ($p > 0.14$ for all t-tests on pairwise differences of log-transformed data). Callieri et al. (1991) also found that chlorophyll and particulate organic C sank at similar rates in a stratified lake in Italy. Sinking rates of suspended pigments varied by 16-fold for the unaveraged data (0.04–0.66) and by fivefold among lake means (0.08–0.40) (Fig. 3). These ranges are similar to those observed by others working in eutrophic lakes exhibiting strong temporal variability in algal biomass (Burns and Rosa 1980; Rathke et al. 1981; Ahlgren 1984; Bloesch and Sturm 1985; Callieri et al. 1991). They are two- to 10-fold smaller than sinking rates of inorganic material (Bloesch and Sturm 1985; Stabel 1987; Callieri et al. 1991).

The response of sinking rates of suspended matter to increases in chlorophyll concentration varied with the fluxing material and between unaveraged and mean data. Sinking rates for suspended pigments did not increase significantly with water column averaged chlorophyll concentrations for either the unaveraged data (slope = 0.0, $p = 0.99$, $R^2 = 0$; Fig. 3A) or the lake means (slope=0.17, p=0.08, $R^2 = 0.09$; Fig. 3B). These results suggest that algae do not sink faster

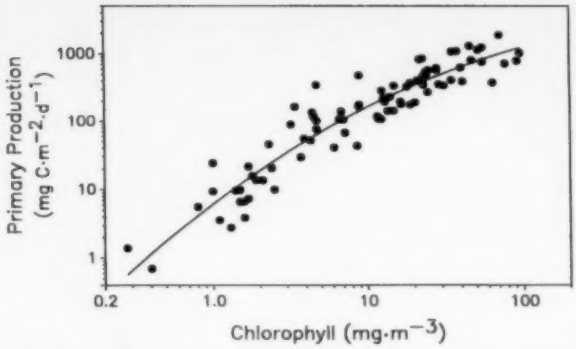

FIG. 4. Relationship between primary production and euphotic zone chlorophyll concentration (equation 5 in text). Regression fitted to data presented by Smith (1979).

in more productive lakes. C sinking rates did not increase significantly with chlorophyll for the unaveraged data (slope = 0.15, $p = 0.03$, $R^2 = 0.07$), but did increase for the lake means (slope = 0.24, $p = 0.003$, $R^2 = 0.43$). N sinking rates exhibited the same pattern as did the C sinking rates. The slopes on the lake mean regressions indicate a 1.75-fold increase in C and N sinking rate for every 10-fold increase in chlorophyll. Thus, the mean data imply that detrital particles which do not contain pigments sink faster in more productive lakes. Generally, however, the concentration of particulate matter was not well related to sinking rates.

The mean sinking rate of suspended particles possibly could have been higher had we sampled communities of particles composed primarily of diatoms or fecal pellets. The maximum sinking rate reported here (0.66 $m \cdot d^{-1}$) is several times smaller than maximum sinking rates periodically exhibited by large physiologically stressed diatoms (Sommer 1984; Takamura and Yasuno 1988) and up to 10 times smaller than the sinking rates of zooplankton fecal pellets (Ferrante and Parker 1977). Usually, however, diatoms sink less than 1 $m \cdot d^{-1}$ (Reynolds et al. 1982; Reynolds 1984; Sommer 1984; Davey 1988; Takamura and Yasuno 1988), while other taxa which were more common in our samples typically sink at rates similar to or less than our mean estimate of 0.2 $m \cdot d^{-1}$ (Ahlgren 1984; Reynolds 1984; Sommer 1984; Trimbee and Harris 1984; Takamura and Yasuno 1988). Furthermore, the sinking rate of suspended particles is expected to be lower than the sinking rate of settled particles, since some suspended particles do not contribute to downward flux (Burns and Rosa 1980). Therefore, the sinking rates reported here agree reasonably with findings from previous studies.

General Implications

It is widely held that a greater fraction of phytoplankton production should sink out of the water column in more productive pelagic ecosystems (Eppley and Petersen 1979; Reynolds 1984; Harris 1986). In this study, we have found that the sinking flux of C in lakes is closely related to water column chlorophyll concentrations. Chlorophyll can also be used to predict seasonal primary production in lakes (Smith 1979). In the following analysis, we determine if these two chlorophyll-based relationships are consistent with a greater loss of phytoplankton production in more productive lakes.

TABLE 5. Export ratios estimated for lakes in this study. Values in parentheses are the number of observations.

Lake	Secchi depth (m)	Euphotic depth (m)	Area primary production (mg C·m^{-2}·d^{-1})	Export ratio (%)
Bull Pond	3.5 (1)	8.4[a]	592	26.6
East Twin	4.4 (4)	10.7[a]	971	29.1
Gilead	3.8 (1)	9.2[a]	1743	10.9
Giles	12.5 (12)	19.3 (12)	264	34.2
Iron Mine Pond	5.2 (1)	12.4[a]	660	24.0
Lacawac	4.1 (12)	6.4 (12)	507	46.6
Minnewaska	9.4 (1)	18.6[b]	96	42.5
Popolopen	3.2 (1)	7.7[a]	483	41.7
Tyrell	2.4 (4)	5.8[a]	1878	17.6
Upton	3.7 (4)	8.8[a]	1660	21.9
Waynewood	2.5 (12)	3.6 (12)	692	44.2
Wonunscopomuc	5.0 (4)	11.9[a]	525	47.2

[a]Euphotic zone depth = 2.4 times Secchi depth (Beeton 1957).
[b]Euphotic zone depth from epilimnetic chlorophyll after Carlson (1977).

Smith (1979) summarized annual means of euphotic zone chlorophyll concentration (Chl, milligrams chlorophyll per cubic metre) and volumetric primary production (PP, milligrams C per cubic metre per day) from 83 lakes located mostly in temperate North America and Europe. A linear regression of the log-transformed data revealed a systematic nonlinearity which could be accounted for with a binomial model of the form $\log Y = a + b(\log X) + c(\log X)^2$ (Fig. 4; p for $b < 0.0001$, p for $c = 0.0006$, F-test based on partial sums of squares):

$$(4)\quad \log \mathrm{PP} = 0.79 + 1.7 \log \mathrm{Chl} - 0.27 (\log \mathrm{Chl})^2,$$
$$R^2 = 0.89,\ p < 0.0001.$$

This model is only a description of the variability in primary production over the range of the data and is not a general physiological representation. We can predict export ratios by substituting output from equation 4 into equation 3 along with estimates of the euphotic zone depth and C sinking flux.

A plot of the export ratio predicted for the study lakes using equation 3 versus primary production suggests that the export ratio should decrease with increasing productivity (Table 5; Fig. 5). Of the C fixed, 30–50% should sink out of the water column in the more oligotrophic lakes whereas only about 10–30% should sink as production approaches 1500 mg C·m^{-2}·d^{-1}. Direct measurements of primary production and sinking flux from the literature are consistent with a negative relationship between the export ratio and primary production (Table 6; Fig. 5; $t = -1.747$, $p = 0.051$, one-tailed test, data not transformed).

To compare the rate at which C sinking flux and primary production increase with chlorophyll, we have regressed C sinking flux against chlorophyll concentrations averaged over the water column:

$$(5)\quad \log S_C = 1.81 + 0.62 \times \log \mathrm{Chl},$$
$$R^2 = 0.83,\ p < 0.0001.$$

A comparison of equations 4 and 5 reveals that the increase of sinking flux with chlorophyll is less steep than the concomitant increase in primary production (Fig. 6). As chlorophyll increases from 0.3 to 3.0 mg·m^{-3}, the ratio of S_C:PP decreases by over 7.6-fold (Fig. 5). According to Carlson (1977),

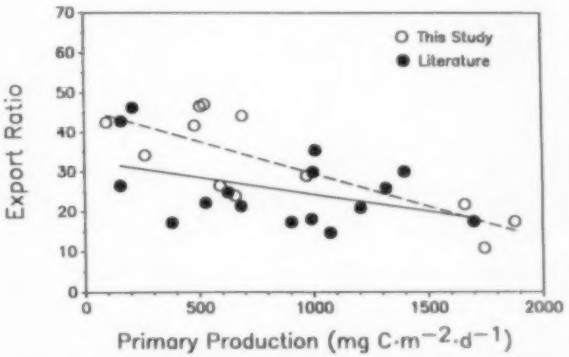

FIG. 5. Percentage of planktonic primary production lost to sinking (export ratio) with respect to primary production as predicted from our data (data = open circles, regression = broken line) and directly observed in other studies (data = solid circles, regression = solid line).

$$(6)\quad \log Z_{\mathrm{Secchi}} = 1.26 - 0.68 \log \mathrm{Chl}.$$

Secchi depth (Z_{Secchi}) decreases by 5.7-fold as surface chlorophyll concentration increases from 0.3 to 3.0 mg·m^{-3} in equation 6. Assuming that euphotic zone depth would decline proportionally to Secchi depth, export ratios are predicted to decline by a modest 32% over the range in chlorophyll in our data.

Sinking fluxes during the spring were not measured in this study. Consequently, the generality of our sinking flux model may be compromised, since the sedimentation of diatoms often represents a major fate for planktonic primary production in spring (Harris 1986; Scavia and Fahnenstiel 1987; Fitzgerald and Gardner 1993). However, the published data used to test the model predictions included 11 instances in which sinking fluxes during the spring period were measured (Table 6). Our predictions were, on average, 5–10% higher than the published estimates, which is opposite the trend expected if our models were systematically underestimating sinking fluxes. In any case, for our results to be misleading, spring production by diatoms would have to be an increasing proportion of total annual production

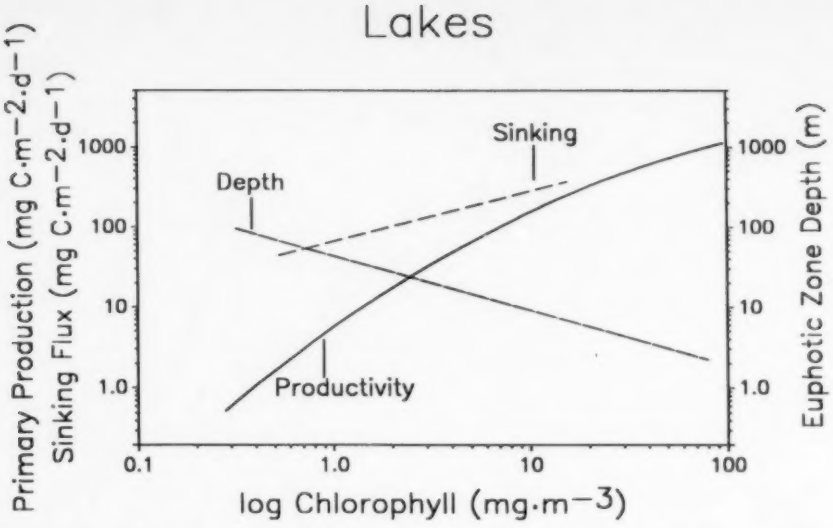

FIG. 6. Models of primary production (equation 3), sinking flux (equation 5), and euphotic zone depth with respect to water column averaged chlorophyll concentrations. The euphotic zone depth is assumed to equal 2.4 times the Secchi disc depth as determined from equation 6 from Carlson (1977).

TABLE 6. Literature observations of phytoplankton primary production and the percentage of phytoplankton primary production lost to sinking in lakes.

Lake	Primary production (mg $C \cdot m^{-2} \cdot d^{-1}$)	Export ratio (%)	Source
Castle, Calif., USA	156	26.3	Kimmel and Goldman 1977
Mirror, N.H., USA	161	42.9	Cole et al. 1989
Konigsee, Switzerland	211	46.4[a]	Stabel 1985
Michigan, USA	381	17.3[a]	Eadie et al. 1984
Lucerne, Switzerland	529	22.3[a]	Bloesch and Uehlinger 1990
Lucerne, Switzerland	1101	14.8[a]	Bloesch and Uehlinger 1990
Michigan, USA	620	25.0	Fahnenstiel and Scavia 1987
			Scavia and Fahnenstiel 1987
Constance, Switzerland			
1980	685	21.5[a]	Stabel 1986
1981	904	17.5[a]	Stabel 1986
Sempach, Switzerland	992	18.2[a]	Bloesch and Uehlinger 1990
Brienz, Switzerland	1000	35.6	Bloesch and Uehlinger 1990
Ontario, USA–Canada	1000	30.0	Charlton 1983
Zug, Switzerland	1205	14.4[a]	Bloesch and Sturm 1985
Lugano, Italy	1315	23.5[a]	Premazzi and Marengo 1982
Hallwil, Switzerland	1317	26.0[a]	Bloesch and Uehlinger 1986
Rotsee, Switzerland	1400	30.1[a]	Bloesch and Uehlinger 1990
Římov, Czechoslovakia	1700	17.6	Porclová 1989

[a]Spring period included.

as lake productivity increases. We know of no empirical evidence for such a shift; on the contrary, anthropogenic nutrient enrichment of lakes would tend to reduce the ratios of Si:P and Si:N and thus may cause diatoms to contribute a smaller fraction to annual phytoplankton production in culturally eutrophied lakes. Direct studies comparing spring and summer phytoplankton losses are warranted to firmly resolve this issue.

Freshwater plankton communities have been hypothesized to retain C less efficiently as they become more productive (Reynolds 1984; Harris 1986). If this were true, the proportion of planktonic primary production lost to sinking of particles should increase with planktonic primary productivity. Our results do not support this expectation. The proportion of phytoplankton primary production lost to sinking appears to decline slightly with lake productivity.

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Stream Channel Morphology and Woody Debris in Logged and Unlogged Basins of Western Washington

Stephen C. Ralph,[1] Geoffrey C. Poole,[2] Loveday L. Conquest, and Robert J. Naiman

Center for Streamside Studies, AR-10, University of Washington, Seattle, WA 98195, USA

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Channel morphology and habitat characteristics of stream segments draining unharvested old-growth forests were compared with those from streams within intensively and moderately logged basins. Sites covered a broad geographic range in western Washington State and were stratified by basin area and channel gradient. Although the number of pieces of large woody debris (LWD) within stream channels was unaffected by timber harvest, there was a clear reduction in LWD size in harvested basins. Timber harvest also resulted in a shift in location of LWD towards the channel margins, outside the low-flow wetted width of the channel. Intensive harvest simplified channel habitat by increasing riffle area and reducing pool area and depth, although the commonly used index of pool-to-riffle ratio appears inadequate to document these changes. Given the natural variation from stream to stream, we conclude that simple counts of instream LWD and channel units (habitat types) are not useful as management objectives. Instead, these attributes should be used collectively as indicators of the complexity and stability of in-stream habitat with respect to the specific channel and valley geomorphology.

Nous avons comparé la morphologie du lit et les caractéristiques de l'habitat dans des segments de cours d'eau drainant des forêts anciennes inexploitées à celles de cours d'eau coulant dans des bassins où l'exploitation forestière est intensive ou modérée. Les sites couvraient une vaste zone géographique dans l'ouest de l'État de Washington, et ont été stratifiés selon la superficie du bassin et le gradient du lit. Le nombre de morceaux de gros débris de bois (GDB) dans les chenaux n'était pas modifié par la coupe du bois, mais on observait une nette réduction de la taille des GDB dans les bassins exploités. La présence de coupes de bois déplaçait aussi la localisation des GDB vers les marges des chenaux, à l'extérieur de la largeur mouillée du lit mineur. L'exploitation intensive simplifiait l'habitat du chenal en accroissant la superficie des radiers et en réduisant la superficie et la profondeur des fosses, mais l'indice couramment utilisé du rapport des radiers aux fosses ne semble pas permettre de rendre compte de ces modifications. Étant donné la variation naturelle d'un cours d'eau à l'autre, nous concluons qu'un simple dénombrement des GDB dans le cours d'eau et des unités de lit (types d'habitat) ne constituent pas des éléments utiles comme objectif de gestion. Ces attributs pourraient plutôt servir collectivement comme indicateur de la complexité et de la stabilité de l'habitat lotique par rapport à la géomorphologie particulière du lit et de la vallée.

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Past and present timber harvesting in steep forested watersheds of the Pacific Northwest triggers physical processes leading to changes in the characteristics of stream channels and aquatic habitat. Basin-level disturbances associated with repeated cycles of timber harvesting alter fundamental characteristics of basin hydrology, sedimentation, and channel structure (Harr 1986; Hartman and Scrivener 1990; Chamberlin et al. 1991; Webster et al. 1992). For example, hill-slope erosional processes caused by harvesting and road construction activities often accelerate the input of sediment into streams (Cederholm et al. 1981; Reid and Dunne 1984). This input changes the sediment transport processes with consequent effects on channel shape through bank erosion (Andrews 1982) and bed scour and deposition (Madej 1978; Hassan 1990). As a result of these collective processes, occurring over many decades and distributed over broad areas of the Pacific Northwest, the cumulative effect of broad-scale timber harvesting on channel morphology, in-stream habitat, and aquatic ecosystems is an issue of considerable concern (Naiman 1992).

In Washington State, commercial forest lands cover 71 225 km^2 or 41% of the land area, equally divided between public and private ownership (Anderson and Bagger 1988). This same landscape encompasses nearly 17 000 km^2 of stream channels supporting important aquatic systems. Managing to mitigate deleterious effects on terrestrial and aquatic resources has been the cornerstone of a state regulatory policy towards timber harvest on state and private lands for over two decades. Yet there has been little effort to account for the physical changes imposed on stream channels and salmonid habitats by widespread historical and contemporary timber harvesting. The ecological significance of these changes to aquatic resources has not been fully described. If such changes are widespread, however, they may entail far-reaching

[1]Present address: Natural Resources Consultants, 4055 21st Ave. West, Seattle, WA 98199, USA.

[2]Present address: Flathead Lake Biological Station, The University of Montana, 311 Bio Station Lane, Polson, MT 59860, USA.

implications for Clean Water Act compliance (MacDonald et al. 1991), the overall biotic integrity of stream systems (Karr 1991), and the sustainability of salmonids in the Pacific Northwest (Nehlsen et al. 1991).

A key component of forested streams altered by harvest practices is the reduction of and altered distribution of wood (Bilby and Ward 1991). Large woody debris (LWD) within streams was once among the most obvious features of forested streams of the Pacific Northwest (Sedell et al. 1984; Hartman and Scrivener 1990). The influence of LWD on local channel hydraulics (as obstructions to flow) and on the storage and transport of sediment in large part determines the physical morphology of the channel. This includes the complexity, spatial array, and hydraulic stability of habitat features, especially pools (Keller and Swanson 1979; Maser et al. 1988; Bilby and Ward 1991). Aquatic communities in general and salmonids in particular depend on a stable and complex mix of such habitat features formed by LWD (Murphy et al. 1984; Grette 1985). Yet the input and residency of LWD in the channel are reduced over time as riparian forests are harvested or otherwise altered (Grette 1985; Hogan 1986; Murphy and Koski 1989).

While these biophysical changes and the management processes involved are reasonably well understood (Hicks et al. 1991), their magnitude and significance at the regional landscape level are poorly described. Both before-and-after case studies (Hartman and Scrivener 1990) and paired watershed studies of harvested versus unharvested watersheds (Hogan 1986) have added greatly to our understanding of the cause-and-effect relationships between timber harvesting and stream habitat for individual basins. However, attempts to apply lessons learned from these limited geographic settings to large-scale regional forest land management have been limited. This in part is due to our poor understanding of the inherent and regional variability of in-stream parameters associated with contrasting geology, climate, and potential vegetation (Hilborn and Walters 1981; Hughes et al. 1986) and by fundamental limitations of experimental design (Quinn and Dunham 1983; Carpenter 1990; Hicks et al. 1991).

Recent efforts by public and private forest land managers to account for the cumulative effects of timber harvest on channel stability and on in-stream habitat at a landscape scale have involved the use of extensive field surveys. These methods attempt to give a synoptic overview of current channel and riparian conditions by surveying stream characteristics presumed to be sensitive to disturbance (MacDonald et al. 1991; Conquest et al. 1994). Although stream surveys have been routinely conducted in forested streams throughout the Pacific Northwest for nearly two decades, there are no published accounts that relate land use to an assessment of stream channel and habitat conditions analyzed at large basin (>100 km^2) scales. Analysis and interpretation of this type of data are also hampered by a lack of historical baseline data, objective criteria, or measurable standards with which to compare the relative condition of streams in harvested basins. Substantive conclusions about the results of surveys cannot be made without some basis from which to judge the nature and ecological significance of these changes to the integrity of the aquatic communities. Such information is essential to development of a reliable means to predict aquatic ecosystem response to repeated disturbances coincident with timber harvest cycles and potential for recovery (Kelly and Harwell 1990). Without such ability, the management of riparian and aquatic resources will substantially fail in its purported promise of wise stewardship.

Our objective was to examine the impacts of forest land management on in-stream aquatic habitat characteristics in geographically diverse basins. We analyzed variables which reflect current channel and habitat conditions from a broad array of streams from managed basins within Washington State and compared these variables with unharvested (old-growth) basins. Our hypotheses are that (i) timber harvest within basins changes the relative proportion and character of pools and riffle habitats in streams and (ii) the size and functional role of LWD in forming in-stream habitats are altered by timber harvest.

Methods

Database Description

Information from 245 stream segments (i.e., study sites) from 101 streams located throughout Washington State was collected during the summers of 1989–91 as part of a general project to characterize channel and habitat conditions. Because of limitations in access and personnel, study sites were not always continuous, and in some cases only limited portions of a given stream were sampled. Segment length, dictated by geomorphically homogeneous reaches of stream, varied from 0.2 to 3.4 km. The study sites (segments) for the larger database were originally delineated using a valley segment criteria (Cupp 1989; see also Frissell et al. 1986; Naiman et al. 1992) where discrete stream lengths are determined on the basis of categories that account for relative channel and valley side slope gradient, geology, the ratio of the active channel width to the valley bottom width, and stream order. In this classification system, (1) F-type segments are generally low-gradient (<1%) alluviated reaches unconfined by steep side slopes, (2) M-type segments are of moderate gradient (1–4%) occasionally constrained by the toe of side slopes, (3) U-type segments flow through glacially carved valleys, (4) V-type segments are usually steep and highly confined by side slopes, and (5) H-type segments are headwater streams with steep gradient, generally intermittent to first order.

For our analyses, we stratified segments on the basis of channel gradient and basin area (as a surrogate for stream size) taken from 1:24000 U.S. Geological Survey topographical maps and channel width (from field measurements) (Table 1). Our preliminary analysis showed that many of the stream characteristics were affected by both basin area and channel gradient. If a valid comparison of sites from different timber harvest regimes were to be made, the distribution of basin area and slope within each group had to be comparable. The range of basin areas (<16 km^2) and stream gradients (<12%) available from the unharvested sites determined the criteria for selection of comparable stream segments. In total, 72 stream segments from 36 streams met these criteria.

Our focus was on LWD as a hydraulic obstruction that traps sediment and forms pools within streams rather than as an attribute related to riparian community structure. Our site selection criteria allowed us to assume that regional differences in basin orientation and related site conditions that determine the composition and stand character of forest communities were not a significant influence on the recruit-

ment and retention of LWD in streams or in our assessment of pool area and depth. Riparian areas adjacent to both reference and treatment sites were historically dominated by large-diameter (>50 cm) conifer trees; and LWD was a persistent and characteristic feature of the streams prior to the onset of forest management and timber harvesting. Regardless of their location, all of these streams had substantial amounts of LWD prior to the expansion of commercial-scale harvesting in the last 50 yr.

Macrohabitat unit types (Bisson et al. 1982) were identified for each stream segment and their surface dimensions measured. Pools were generally characterized by depressions in the stream bed where velocities were slowed; riffles were characterized as shallow areas of from 1 to 4% in gradient and flat cross-sectional profile where stream flow velocities were relatively uniform and bedload particle sizes were relatively homogeneous, and cascade units were areas >4% in gradient where velocities were high, bed mateial coarse, and surface flow highly turbulent. Residual pool depth was defined as the difference between maximum pool depth and the pool crest outlet depth (approximates depth at stage of zero flow), measured for each pool (Lisle 1987). Bank-full width was measured between the vertical points on each bank that indicated normal high water level (Dunne and Leopold 1978).

Measurements of the number, size, and position of in-channel LWD were also included. LWD was defined as any log at least 0.1 m in diameter and 3 m in length. Size of LWD pieces was accounted for by placing into one of two size classes by diameter: 0.1–0.5 and >0.5 m. Unfortunately, this categorical size data precluded a reliable means of determining overall LWD volume. Only LWD positioned within the bank-full width of the channel was surveyed. In log jams with more than 10 pieces, the number and size of debris pieces were estimated because of the practical limitations of seeing pieces buried within the debris pile. A complete description of the contents of the database and the field methods used can be found in Ralph et al. (1991).

Study Area Description

The topography of the western Washington basins encompassing the study areas is steep and irregular with basin elevations ranging from sea level to 1000 m. Beginning and ending points for study sites were typically below 400 m in elevation. Average annual precipitation for the study areas ranged from 100 to 400 cm/yr. The unharvested reference sites were from Olympic Peninsula coastal drainages or from elevations >300 m on the west slope of the Cascade Mountains. Typically the reference sites received more precipitation (>300 cm/yr) than treatment sites located at lower elevations, especially those in the intensive harvesting category (<200 cm/yr). Dominant geologic units included unconsolidated glacial deposits, volcanic (lower Tertiary), and sedimentary rocks in higher elevations of the Cascades. Dominant vegetation within lower elevation basins included western hemlock (*Tsuga heterophylla*), Douglas-fir (*Pseudotsuga menziesii*), and western red cedar (*Thuja plicata*) with a transition to silver fir (*Abies amabilis*) at elevations >600 m. Steam segments in basins where timber harvesting has occurred within the last 80 yr typically had riparian zones dominated by deciduous trees (*Acer macrophyllum* and *Alnus rubra*), while unharvested sites were dominated by conifers >80 yr of age.

Designation of Harvest Intensity Categories

We divided sample sites into three harvest categories (intensive, moderate and unharvested) based on information available about the history of timber harvest within their respective drainage basins. In assigning stream segments to harvest categories, we assumed they would manifest cumulative effects of basin-wide timber harvesting in measurable ways, based on the fact that stream channels must adjust to changes in the input and routing of sediment and flow. Basin-wide clear-cutting can substantially alter the input of sediment (Cederholm et al. 1981) and basin discharge regime (Harr 1986). Due to limitations in the original database, our intensive sites were concentrated in one general area, while sites within the other two categories were more geographically diverse.

Unharvested

Unharvested (control) sites were in basins where no timber harvest activity or road construction has occurred. Under federal administrative protection, these sites included second- to fourth-order tributaries to the White Chuck River (tributary to the Sauk River, draining portions of Glacier Peak Wilderness Area) and the Hoh River and Quinault River basins (Olympic National Park). None of the basins encompassing these sites showed evidence of recent major natural disturbances (fire, windstorms, etc.) and all had mature stands of coniferous forest.

Moderate

Moderately harvested sites were geographically dispersed in basins under government ownership or under mixed government/private ownership. Although forestry had been the dominant land use in these basins, these sites were characterized by relatively moderate levels of timber harvest (<50% of the basin harvested in the past 40 yr) and of road construction and by long reaches of unharvested or age 40+ yr riparian stands. Mature riparian forest (80+ yr) bordered at least 50% of the lineal length of 13 of the 29 segment sites, while the remainder had age 40+ riparian vegetation. No information on road density with these basins was readily available at the time.

Intensive

Intensively harvested sites were in basins that had a combination of high road density and >50% of the basin area clear-cut harvested within the past 40 yr. All but three of our sites were within the upper portion (157 km^2) of the Deschutes River basin of western Washington, with >80% of this basin in private ownership. Average road density in the upper basin exceeded 3.7 km road/km^2 basin versus an average drainage density of 2.5 km/km^2 for western Washington basin. Approximately 63% of the Deschutes watershed had been clear-cut from 1950 to 1986, and 44% was harvested from 1974 to 1986 after the onset of forest land management regulations. Since 1974, harvest intensities within subbasins encompassing our sites ranged from 11 to 65% of their respective areas. Several areas had been previously harvested early in this century (Sullivan et al. 1987). Of the 25 recent or active landslides within the Deschutes basin, 80% of them originated within areas harvested during the last 16 yr (Toth 1991). Three sites on McLane Creek (Fig. 1) were also included in this category because of a similar disturbance history (deforested and converted to agricultural purposes). The riparian zones of all but two of the 15 sampled

TABLE 1. Characteristics of surveyed stream segments by management category.

	Stream	Basin	Segment type	Stream order	Length (km)	Area (km^2)	Channel gradient (%)
Intensively harvested sites	Fall Cr.	Deschutes	F4	3	0.6	7.5	6.1
	Huckelberry Cr.	Deschutes	M1	3	1.1	5.4	3.2
	Huckelberry Cr.	Deschutes	M1	3	0.6	4.1	4.0
	Huckelberry Cr.	Deschutes	V1	3	0.5	5.0	4.6
	Huckelberry Cr.	Deschutes	V1	3	0.8	3.0	5.4
	Huckelberry Cr.	Deschutes	V3	3	0.5	4.4	4.4
	Johnson Cr.	Deschutes	M1	4	0.8	5.7	2.6
	Thurston Cr.	Deschutes	M1	3	1.0	12.1	2.6
	Thurston Cr.	Deschutes	V2	3	0.8	11.3	1.8
	Lincoln Cr.	Deschutes	M2	3	3.1	11.0	5.1
	Lewis Cr.	Deschutes	V1	2	2.1	4.6	5.4
	Ware Cr.	Deschutes	V2	3	0.8	2.9	8.4
	McLane Cr.	Puget Sound	H2	3	0.6	3.2	6.4
	McLane Cr.	Puget Sound	M1	3	2.1	7.6	4.4
	McLane Cr.	Puget Sound	M2	3	2.3	10.7	1.1
Moderately harvested sites	Muddy Cr.	Sauk R.	M1	3	1.8	7.8	3.2
	All Cr.	Sauk R.	M1	2	0.8	10.3	5.4
	All Cr.	Sauk R.	U3	2	0.5	7.6	11.0
	M.F. Taylor	Cedar R.	F4	3	1.1	15.3	2.2
	S.F. Taylor	Cedar R.	F4	2	1.1	5.3	1.4
	Charley Cr.	Green R.	H1	3	1.0	3.4	8.3
	Charley Cr.	Green R.	V1	3	1.3	11.7	4.7
	Charley Cr.	Green R.	V2	3	1.6	6.0	6.8
	Perry Cr.	Puget Sound	M1	3	0.6	13.6	2.1
	Perry Cr.	Puget Sound	M2	3	0.5	15.5	1.8
	Perry Cr.	Puget Sound	V3	3	0.3	13.3	5.5
	Skookum Cr.	Puget Sound	M1	4	0.5	4.0	5.5
	Skookum Cr.	Puget Sound	M2	4	1.1	8.3	1.7
	Skookum Trib.	Puget Sound	M1	3	0.2	2.5	5.6
	Dowans Cr.	Bogachiel R.	M2	3	3.4	10.5	2.8
	Tower Cr.	Hoh R.	M1	2	1.5	3.7	8.8
	Maple Cr.	Hoh R.	M1	3	1.6	8.0	4.1
	Maple Cr.	Hoh R.	V3	3	3.5	5.6	7.7
	Spruce Cr.	Hoh R.	F3	3	0.8	3.2	0.9
	Canyon Cr.	Hoh R.	M1	2	1.6	3.1	8.7
	Canyon Spr.	Hoh R.	F3	3	0.3	0.5	3.5
	Iron Maiden Cr.	S.F. Hoh	F5	3	0.3	1.5	3.9
	Brittain Cr.	Humptulips R.	F5	3	0.8	13.8	0.4
	Brittain Cr.	Humptulips R.	M1	3	1.0	14.1	0.6
	Brittain Cr.	Humptulips R.	M1	3	1.1	11.9	1.9
	Brittain Cr.	Humptulips R.	V3	3	1.1	15.0	2.0
	Elwood Cr.	Humptulips R.	V1	2	1.5	4.4	1.4
	Unnamed	W.F. Satsop R.	F5	4	0.8	6.6	1.7
	Unnamed	W.F. Satsop R.	M2	4	1.6	6.0	4.0
Unharvested sites	Camp Cr.	White Chuck R.	V1	2	2.9	11.1	3.1
	Camp Cr.	White Chuck R.	V4	2	0.6	11.5	2.6
	Camp Cr.	White Chuck R.	V4	2	0.3	9.7	1.9
	Pumice Cr.	White Chuck R.	M1	3	0.3	5.9	3.5
	Pumice Cr.	White Chuck R.	M2	3	1.1	5.8	2.6
	Pumice Cr.	White Chuck R.	U4	3	1.0	5.4	4.9
	S.F. Tunnel	Quilcene R.	V4	2	1.4	13.4	6.4
	Split Cr.	S.F. Hoh R.	F5	3	2.1	2.0	1.9
	Split Cr.	S.F. Hoh R.	M1	3	2.4	2.0	6.7
	Shelter Cr.	S.F. Hoh R.	F5	3	0.6	4.0	2.5
	Camp Cr.	S.F. Hoh R.	F4	2	1.3	11.1	1.2
	Camp Cr.	S.F. Hoh R.	V2	2	0.3	10.9	9.7
	Camp Cr.	S.F. Hoh R.	V3	2	1.3	10.8	7.7
	W. Twin Cr.	Hoh R.	F4	3	0.8	5.9	3.0
	Twins Cr.	Hoh R.	M1	4	0.8	7.7	1.1
	509	Hoh R.	U1	3	1.0	6.0	1.0
	Springs Cr.	Hoh R.	F5	2	0.3	1.1	1.3
	Jackson Cr.	Hoh R.	F4	2	1.3	13.9	5.7
	Jackson Cr.	Hoh R.	V3	2	1.3	13.7	10.1

TABLE 1. (*Concluded*)

Stream	Basin	Segment type	Stream order	Length (km)	Area (km^2)	Channel gradient (%)
Cougar Cr.	Hoh R.	F5	2	1.0	2.3	2.0
Unnamed	Hoh R.	F4	?	1.9	13.5	0.7
Willaby Cr.	Quinault R.	M1	2	0.2	9.8	3.1
Willaby Cr.	Quinault R.	M1	2	0.5	9.2	2.8
Willaby Cr.	Quinault R.	M1	2	0.8	6.8	2.3
Willaby Cr.	Quinault R.	M2	2	0.2	9.3	1.3
Willaby Cr.	Quinault R.	M2	2	1.3	8.9	1.4
Willaby Cr.	Quinault R.	V2	2	0.5	6.4	10.4
Zeigler Cr.	Quinault R.	U1	2	1.6	6.8	4.5

reaches in this category showed dominant stand age (75% of segment length) of less than 40 yr.

Statistical Treatments

Stream segment length varied, since stream morphology determined segment end points and hence, no provision for minimum necessary segment size was made prior to data collection. We therefore used the estimate of variance from each stream segment to calculate, for each stream characteristic analyzed, the minimum stream segment length necessary to be 90% confident that the observed mean was within 12.5% of the population mean (for description of calculations, see Zar 1984). If a segment length was less than the calculated minimum required length for an analysis, the segment was excluded from that analysis. Some segment lengths were sufficient for only some of the analyses. Therefore, number of segments used in each analysis varies.

The statistical analysis of pieces of LWD per stream kilometre, fraction of LWD >50 cm in diameter, fraction of stream area in pools, riffles, and cascades, mean residual pool depth, within-stream variance of residual pool depth, and mean pool area was similar. Within-site mean values or fractions were calculated for each segment. These values were then used to calculate the grand mean (mean of the segment means or fractions), SD of the grand mean, median, and range for each timber harvest category. A one-way ANOVA and, if significant differences at $\alpha = 0.10$ were found, a Tukey test were performed to determine differences between harvest categories. Segment means were then plotted against channel width, basin area, and/or stream gradient for each harvest category. If the slope of any of the resulting regressions was significantly different from zero at $\alpha = 0.10$, the regressions were used to adjust segment-level means or fractions and statistically eliminate differences between harvest groups that were the result of differences in basin area or stream gradient. The grand mean, SD, median, and range were then calculated and plotted for these adjusted data, and an ANOVA and Tukey test were again performed.

The distribution of woody debris within the channel was also analyzed. Grand mean SD, median, and range were calculated, as above, for the fraction of LWD located in each of four locations relative to the low-flow wetted width of the channel: outside wetted width, partially within wetted width, wholly within wetted width, and bridging channel. A multiresponse permutation procedure (Zimmerman et al. 1985) was then used to establish if the distribution of LWD among these four locations differed significantly among the three harvest categories.

Results

LWD versus Stream Size

We examined the number of pieces of LWD for each of three harvest categories with sites stratified alternatively by bank-full width and then basin area as surrogates for stream size (Fig. 2). The data showed no significant difference ($P = 0.24$) in the mean number of pieces of LWD per 1000 m of stream among the three harvest categories when stratified by either bank-full width or basin area.

However, there were clearly fewer large-sized pieces of LWD in basins where logging has occurred (Fig. 3). Unlogged stream segments had a higher fraction of overall woody debris in the larger size category than did sites from moderately or intensively harvested basins ($P < 0.01$). Figures 2 and 3, taken together, support the hypothesis that wood volume was more sensitive to timber harvest than a simple count of wood frequency. The effect of stream size on size distribution of LWD was evaluated when the fraction of LWD >50 cm in diameter was plotted against bank-full width and basin area. Bank-full width had no affect (i.e., slope = 0) on the size class distribution of LWD ($\alpha = 0.1$) regardless of harvest intensity (Fig. 3). However, in unharvested basins, the fraction of LWD in the larger size class (>50 cm in diameter) increased ($P < 0.01$) with increasing basin area. This was in contrast with harvested sites where the relationship of basin area and fraction of large-sized LWD was not significant ($\alpha = 0.1$). This result suggests a disruption in the supply of larger sized pieces of woody debris to stream channels in basins with a history of forest land management. The observed difference between harvest categories remains after adjusting for the effects of basin area.

Habitat Area

The relative proportion of stream area in pools, riffles, or cascades is considered a meaningful indication of in-stream habitat condition (Bisson et al. 1982; Platts et al. 1983). Although some of the inherent variability in habitat area can be accounted for in part by channel gradient (Keller and Swanson 1979), we wanted to determine whether this parameter was sensitive enough to reflect watershed level disturbances associated with timber harvesting when compared with unharvested sites. Data were analyzed to dis-

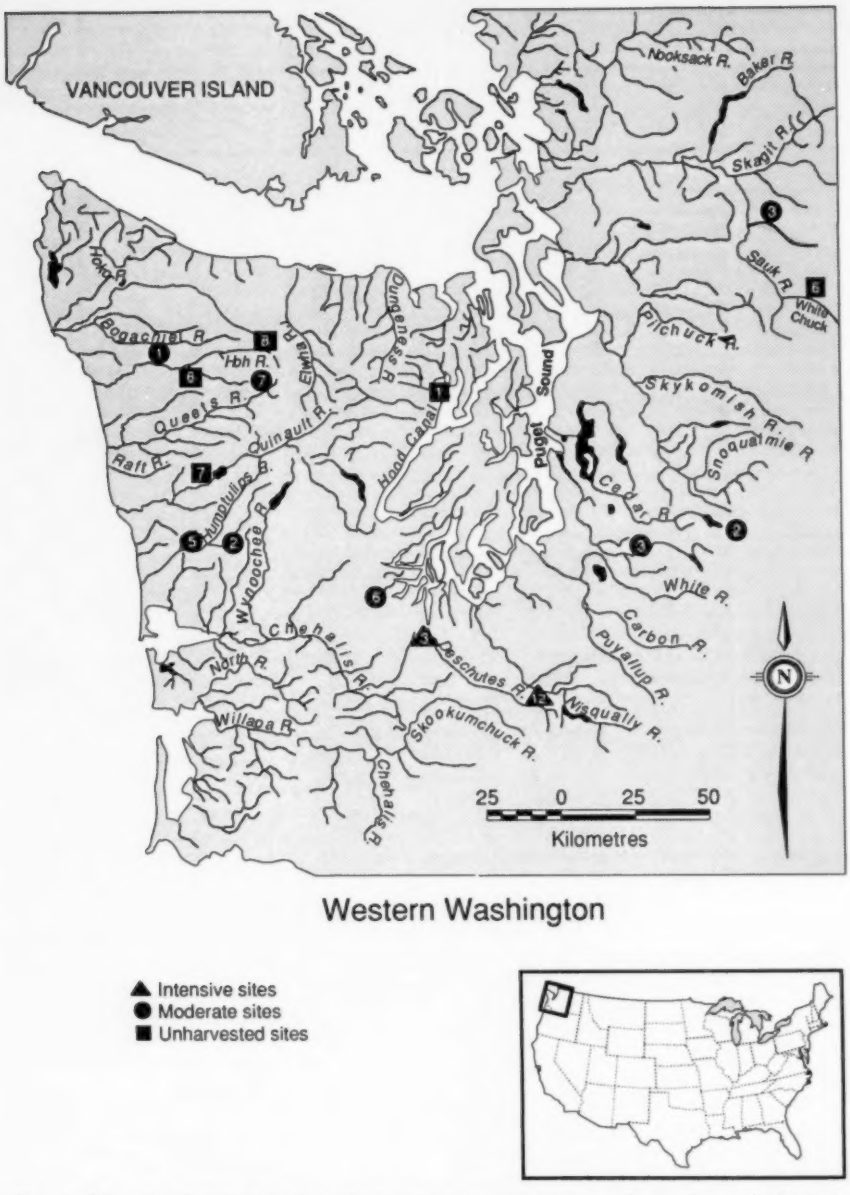

FIG. 1. Map showing river basins where stream segments surveyed were located. Symbols refer to relative degree of timber harvesting within each basin; numbers within symbols refer to the number of discreet sites (stream segments) sampled within each basin.

play the fractional components of each of the three macrohabitat types.

Pools

Intensive timber harvesting significantly decreased the fraction of stream area in pools. The mean fraction of low-flow wetted area comprising pool habitats was different between unharvested and intensively harvested sites ($P = 0.08$; Fig. 4). Gradient alone affected this response variable in unharvested and moderately harvested sites. After statistically adjusting the data to account for differences attributable to gradient, moderately harvested sites also differed from intensively harvested sites. The relationship between pool frequency and gradient was altered for sites in basins intensely harvested as shown by the broken line in the scatter plot for pools in Fig. 4. Pool frequency decreased in low-gradient streams, but was not as affected in high-gradient streams where intensive logging occurs. However, this does not suggest that high-gradient streams were more resistant to the impacts of logging. High-gradient (>8%) streams were dominated by cascade reaches (Fig. 4) with coarse boulder or bedrock hydraulic controls (rather than LWD) and higher

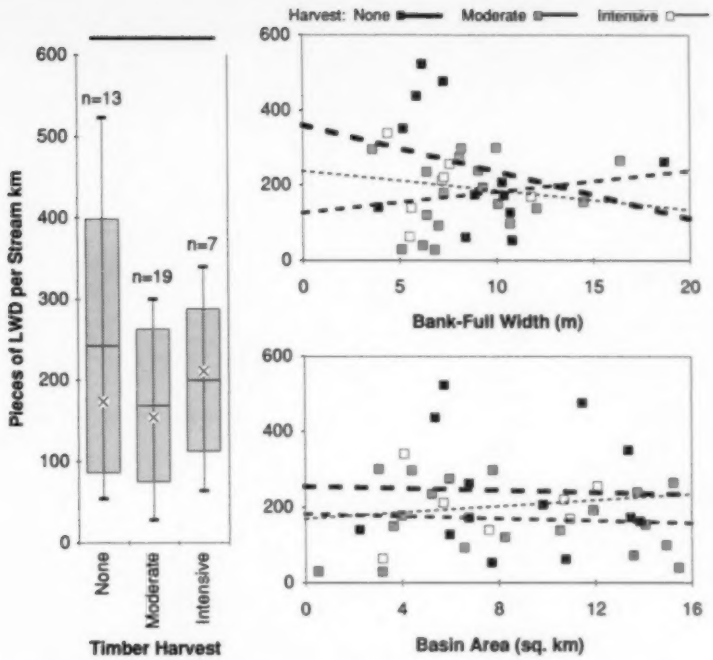

FIG. 2. Number of pieces of LWD per stream kilometre by harvest category. In box plot, boxes show mean ±SD; crosses and bars denote median and range. For ANOVA, $P = 0.24$. In scatter plots, response is plotted versus bank-full width (top) and basin area (bottom). Broken lines represent regression slopes not significantly different from zero (bank-full width: none, $P = 0.35$; moderate, $P = 0.45$; intensive, $P = 0.76$; basin area: none, $P = 0.92$; moderate, $P = 0.75$; intensive, $P = 0.73$).

velocity flow regimes. Pools within these reaches are frequently subject to hydraulic scouring and are less susceptible to being buried under bedload. There are also fewer pools in such streams, and larger sample sizes of pools would be necessary to document any effect. In unharvested and moderately harvested stream sites with gradient <3%, pools account for >50% of wetted area, while in the intensively harvested sites in the same gradient range, they account for <40%. Note also that the variance around the mean was reduced for sites within intensively harvested basins when compared with that for the moderate and unharvested sites. This compression of the variance further supports the generalization that intensive harvesting of forested basins leads to simplification and homogenization of habitat structure.

Riffles

An ANOVA for the unadjusted data on the fraction of stream area comprising riffles showed no significant difference between the various harvest categories (Fig. 4). However, the influence of stream gradient on riffle frequency was significant for all categories. Removing the effect of gradient allowed us to document the effect of timber harvest on riffle frequency. The Tukey test on the adjusted data showed a difference ($P = 0.04$) between streams subject to intense harvest and the other two categories.

Cascades

Timber harvest had little or no effect on the overall proportion of cascade type units for stream reaches of a given channel gradient. There were no significant differences in cascade area between means or variances among sites from all harvest catgories (Fig. 4). Cascade area increased as gradient increased for all harvest classes. Even with the effect of gradient statistically removed, there were no significant differences between sample means and variances.

Habitat Character

Pool depth

Intensive logging in basins appeared to reduce the average depth of pools in streams. Mean residual pool depths among our study sites were lower in intensively harvested basins ($P = 0.02$) than in the other two harvest categories (Fig. 5), irrespective of stream gradient. Gradient did not seem to be an overall determinant of mean residual pool depth for sites irrespective of basin harvest category. In addition, the overall within-stream variance of pool depths was reduced in sites from intensively harvested basins when compared with unharvested sites ($P = 0.02$; Fig. 5).

Pool area

Intensive timber harvest appeared to reduce the overall mean area of pools when compared with sites from moderate and unharvested basins. The mean pool surface area of sample segments from intensively logged sites was different from either the moderate or unharvested sites ($P = 0.01$; Fig. 6). Note also the limited range in overall values and variance for these sites. In spite of similar slopes among the three harvest classes, gradient showed a significant effect ($P < 0.01$) only in intensively harvested streams due to the

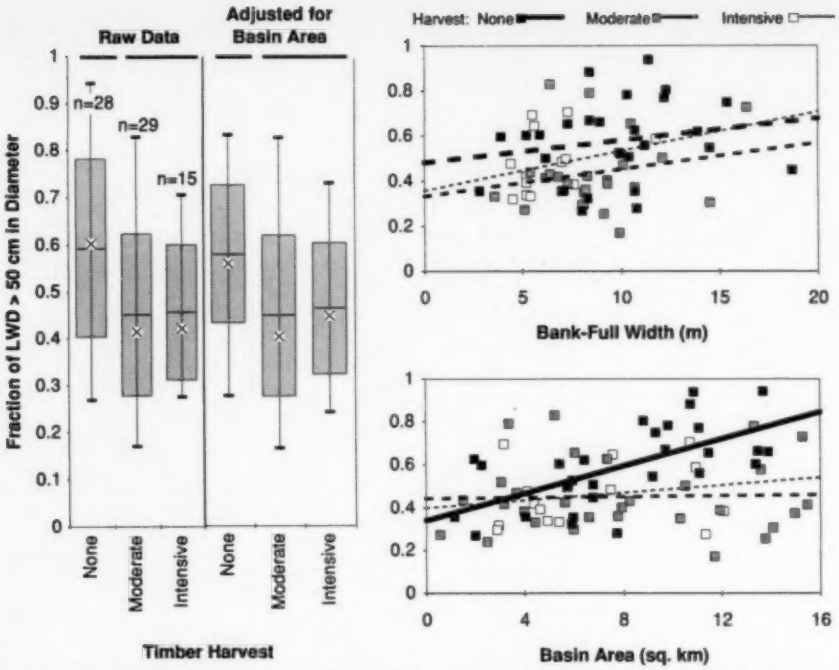

FIG. 3. Fraction of LWD >50 cm in diameter by harvest category. In box plots, boxes show mean ±SD; crosses and bars denote median and range. For ANOVA, $P < 0.01$. Tukey tests were performed at $\alpha = 0.10$. In scatter plots, response is plotted versus bank-full width (top) and basin area (bottom). Broken lines represent regression slopes not significantly different from zero (bank-full width: none, $P = 0.34$; moderate, $P = 0.32$; intensive, $P = 0.40$; basin area: none, $P < 0.01$; moderate, $P = 0.88$; intensive, $P = 0.48$).

very low variance in this category of sites. Statistically adjusting the data for gradient strengthened the observed difference in mean values ($P << 0.01$). The variance decreased considerably for intensively harvested sites, suggesting that most of the variation in the unadjusted data was due to differences in stream gradient. The adjusted data also showed that the observed difference in mean values between unharvested and moderately harvested sites could also be attributed to differences in gradient. Within-stream variance in pool surface area was nearly significant ($P = 0.14$; Fig. 6) and showed a considerable downward trend. We suspect that a larger sample size would document a significant effect.

LWD Position within the Channel

Timber harvesting affects not only the size (Figs. 4 and 5) but the spatial distribution of LWD within the stream channel (Fig. 7). Results of multiresponse permutation procedures show that the distribution of woody debris location is significantly different for all harvest intensities ($P < 0.01$). On average, nearly half of the LWD found in streams of intensively harvested basins is completely outside the low-flow wetted width. Roughly one third interacted with the low-flow channel, but only 6% was contained fully within the channel. In moderately harvested basins (Fig. 7), almost half of the wood interacted with the low-flow channel, but only 19% was fully within. Nearly one quarter of the wood was outside the low-flow channel. In unharvested basins, two thirds of the wood interacted with the low-flow channel; one third was contained fully within. Only 17% of the LWD did not interact with the low-flow channel.

Discussion

Large Woody Debris in Streams

A count of pieces of LWD alone was less sensitive to the effects of harvesting than a survey which included size class distributions or measures of wood volume. Bilby and Ward (1989) and Robison and Beschta (1990) found that the mean frequency of LWD varied with bank-full width in their study of undisturbed old-growth forested basins of southwestern Washington. We did not see a similar relationship in our data.

Two possible explanations for this discrepancy are (1) the more limited geographic distribution of sites used for their data and their use of bank-full width as a measure of stream size and (2) a smaller sample size of LWD counts per stream. Bilby and Ward (1989) examined old-growth streams in a broader range of basin areas and channel gradients (1–18%) and in a more limited geographic area. They relied on bank-full width as a comparative basis for stream size. They arrived at a measure of LWD frequency per metre of stream length by surveying a length of stream sufficient to count 50 pieces of LWD and then dividing by that respective length. In all but one case ($n = 22$) the length of stream was less than 0.5 km. Our data also suggest that substantially more sampling, i.e., longer reaches of stream than is typically used, is necessary to obtain a reliable estimate of in-channel

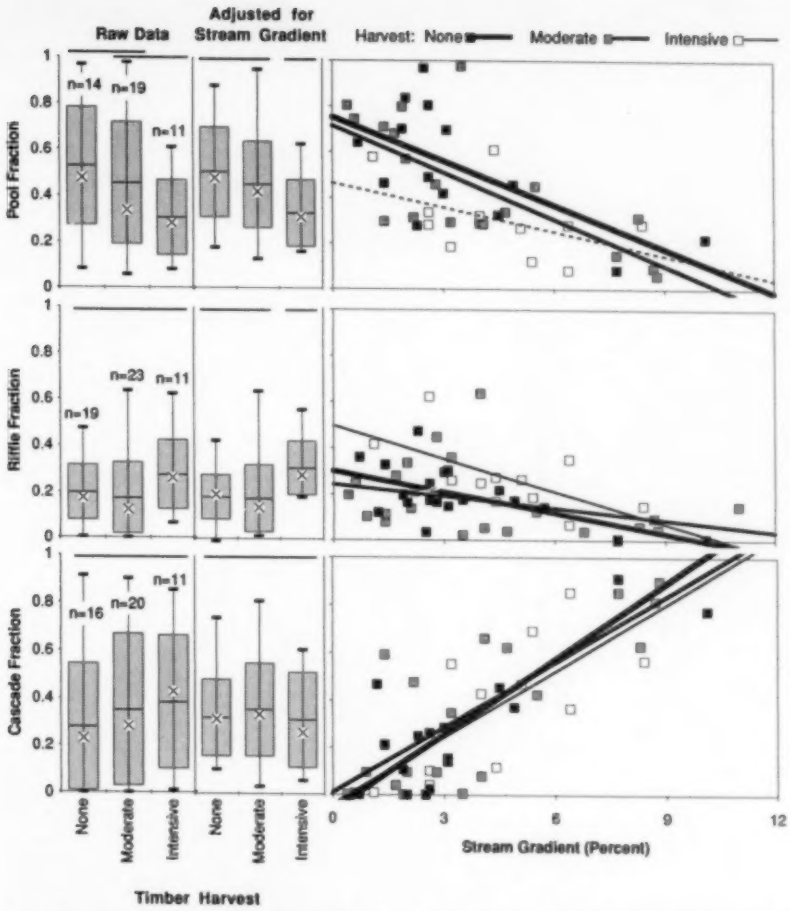

FIG. 4. Fraction of stream area comprising pools, riffles, and cascades by harvest intensity. In box plots, boxes show mean ±SD; crosses and bars denote median and range. Significance levels for ANOVAs were $P = 0.08$, 0.16, 0.63, 0.04, 0.04, and 0.78 for raw pool, riffle, and cascade and adjusted pool, riffle, and cascade fractions, respectively. All performed Tukey tests were at $\alpha = 0.10$. In scatter plots, broken line represents regression slope not significantly different from zero (pool: none, $P = 0.01$; moderate, $P << 0.01$; intensive $P = 0.16$; riffle: none, $P < 0.01$; moderate, $P = 0.10$; intensive, $P = 0.04$; cascade: none, $P << 0.01$; moderate, $P << 0.01$; intensive, $P = 0.02$). Sample numbers vary within harvest categories because some stream segments were not long enough to provide statistically valid estimates of all three fractions.

LWD. The clumped distribution of LWD within streams subjected to basin timber harvesting appeared to result in a high within-stream variance in woody debris frequency. Generally, LWD surveys of 1–2 km were necessary to meet our confidence interval of 90% (±12.5% of maximum).

Stratifying sites by stream size

The use of bank-full width as a way of stratifying sites to analyze LWD frequency and volume is a convention well established in the literature (Bilby and Ward 1989) although its use in basins affected by land use practices is somewhat dubious. Although it is a direct, continuous measure of a stream characteristic, it is not independent of cumulative land use impacts. Alluviated stream channels in general respond to increases in inputs of discharge and sediment by becoming wider and shallower (Dunne and Leopold 1978; Madej 1978). The practice of comparing sites within basins where logging and its attendant activities have occurred for several decades with sites from unharvested basins seems unreliable if the channel geometry has adjusted to altered regimes of sediment input and basin hydrology. Without a reliable method to determine predisturbance channel dimensions (Orsborn 1990), use of channel width as a meaningful way to report LWD volume in basins affected by land used seems inappropriate. We recommend the use of basin area as a more meaningful indicator of stream size when comparing streams with different management histories, especially when they occur in regions with relatively similar geology, drainage density, and precipitation patterns.

LWD size and stability

Our data illustrate that the effect of timber harvesting, whether intensive or moderate, shifts the size class distribution of LWD toward smaller pieces in second- to fourth-

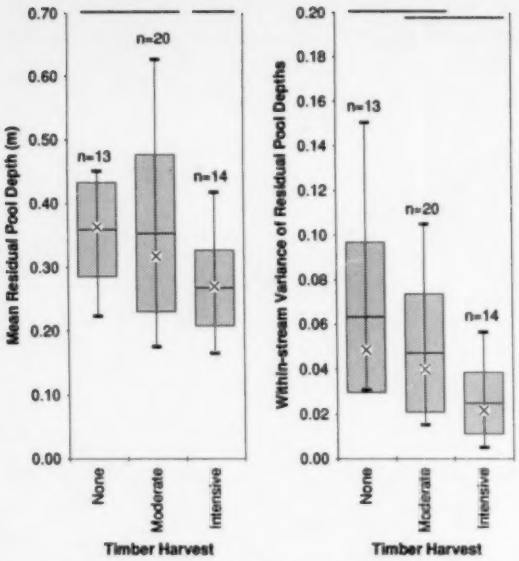

FIG. 5. Mean residual pool depth and within-stream variance of residual pool depth by harvest category. Boxes show mean ±SD; crosses and bars denote median and range. For ANOVAs, $P = 0.02$ for both mean depth and within-stream variance. For Tukey tests, $\alpha = 0.10$.

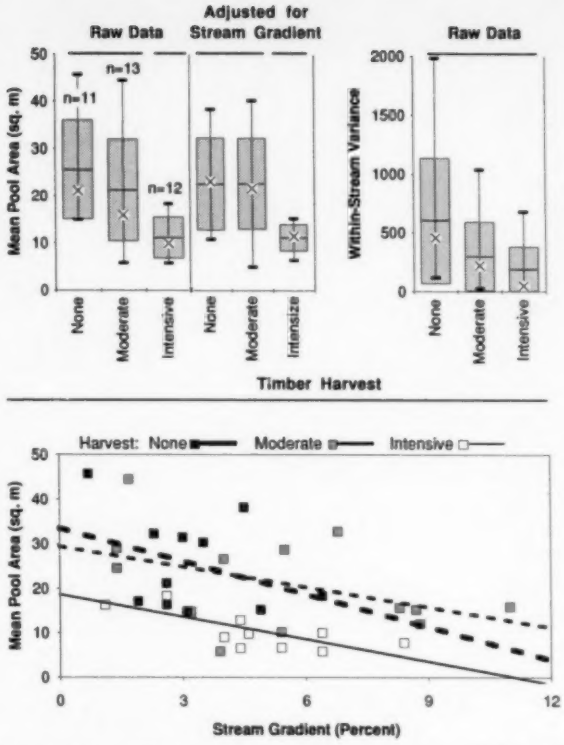

FIG. 6. Mean pool surface area and within-stream variance of pool surface area by harvest category. In box plots, boxes show mean ±SD; crosses and bars denote median and range. For ANOVAs, $P < 0.01$, $P << 0.01$, and $P = 0.14$ for mean pool area, adjusted mean pool area, and within-stream variance, respectively. Performed Tukey tests were $\alpha = 0.10$. In the scatter plot, broken lines represent regression slopes not significantly different from zero ($P = 0.27$, $P = 0.13$, and $P < 0.01$ for none, moderate, and intensive harvest, respectively).

order streams. The minimum size criterion (>10 cm in diameter) that has become the conventional standard applied to defining LWD was originally based on the ease of handling logging slash during stream cleaning operations (Froehlich et al. 1972). Due to the process of LWD recruitment from intact riparian zones made up of large mature coniferous trees, streams from unharvested basins should be expected to typically have larger average-sized LWD. Heiman (1988) noted that in Oregon coastal basins logged without retention of riparian trees, preharvest LWD (when not removed by salvage logging) continued to account for most in-stream wood even 140 yr after harvest. He further noted that the total volume of debris was only 30% of preharvest levels, a finding corroborated by Bilby and Ward (1991).

Effect of harvest practices

Other studies have shown that the primary factor in determining retention and stability of LWD is its size and position (Bilby 1984; Grette 1985; Bisson et al. 1987). However, our data suggest that streams flowing through old-growth forests retained more smaller pieces of woody debris than streams from logged basins. Woody debris appears to be retained within the channel (Fig. 8) regardless of the size, although this may reflect the more active recruitment of such material than is seen in streams from harvested basins, rather than actual long-term retention. In spite of the general shift towards smaller LWD, some moderately harvested sites retain their LWD, but others do not. This may be some artifact of postlogging selective removal of in-stream LWD having commercial value. In intensively harvested basins, LWD diameter appears to control how much debris is retained by the stream. The ability to retain smaller pieces of LWD is generally reduced with intense levels of clear-cut harvest and sometimes reduced with moderate harvest, perhaps reflecting changes in channel geometry, an interruption in woody debris input from the now harvested riparian zone, or postlogging removal for commercial sale of LWD embedded in the channel. Knowledge of the potential debris recruitment from upstream and the adjacent riparian zone and retention over time is crucial to achieve the necessary recruitment from riparian corridors of adequately sized LWD into stream channels, and riparian harvest regulations need to reflect this.

Washington State's current harvesting scheme utilizes a sliding scale system of riparian tree retention on state and private forest lands. Under this rule, few to no trees are retained along riparian areas of headwater (first-order) streams, and coniferous trees left along the riparian zone of larger order streams may take from 60 to 100 yr to attain sufficient size to contribute to stable in-stream LWD (Grette 1985; Bilby and Wasserman 1989). This assumes that such trees will be retained in channels that may have widened in response to changes in basin hydrology and sediment input and transport. Until the mid-1970's, it was a common practice in the Pacific Northwest to remove all merchantable timber from riparian zones and LWD from virtually all stream channels adjacent to a timber harvest, even if such material was stable and provided desirable aquatic habitat features. Prior to 1992, there

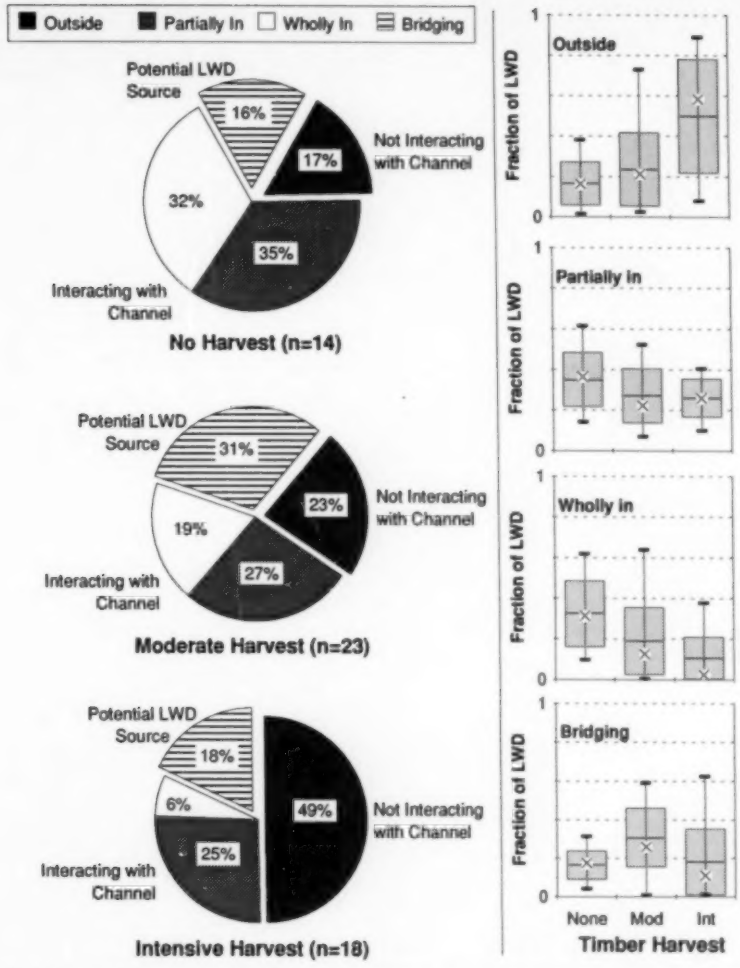

FIG. 7. Mean distribution of LWD location relative to low-flow wetted stream channel. In box plots, boxes show mean ±SD; crosses and bars denote median and range.

were no regulatory restrictions on the size of individual clear-cut or the cumulative area harvested within a basin for a given period.

LWD position

Intensive forest utilization results in LWD that is clumped within the channel and concentrated on the inside of bends, along channel margins, and other areas of reduced velocity. These LWD positions contribute little to habitat complexity during periods of summer low flow. Note the extreme difference in variance between sites for the fraction of LWD outside the channel for the three harvest categories (Fig. 7). For sites from intensively logged basins, the median value shows that nearly half of the sites had 60% or more of the LWD outside the low-flow wetted width, while the moderate and unharvested sites are in the range of 23 and 17%, respectively. Further, the median value of the fraction entirely within the low-flow channel shows that half of the intensively harvested streams had less than 1 in 50 pieces fully within the active low-flow wetted channel. Contrast this with the fact that no unharvested stream had more than 40% of its LWD fully outside the low-flow wetted channel (median = 20%) and every unharvested stream had at least one in nine logs fully within the low-full wetted width (median greater than one in three). This suggests that one consequence of logging, even at moderate levels, is that newly recruited, smaller sized LWD is less hydraulically stable, is more prone to transport within the channel, becomes mobile at frequently occurring winter flows, and is less likely to contribute to habitat structure within the low-flow wetted channel.

The differences in location of LWD within the channel noted by our data (Fig. 7) suggest that mobility of LWD increases in basins with timber harvest. This mobility suggests that timber harvesting in basins increases the instability in both the channel and the habitats formed by LWD. Another consequence of unstable or limited LWD in channels is a reduction in its role in the storage of bedload. This may in part account for the significantly shallower depth of pools in streams from basins under intensive harvest because sediment stored behind LWD is transported downstream during high-flow events, exceeds transport capacity, and fills pools.

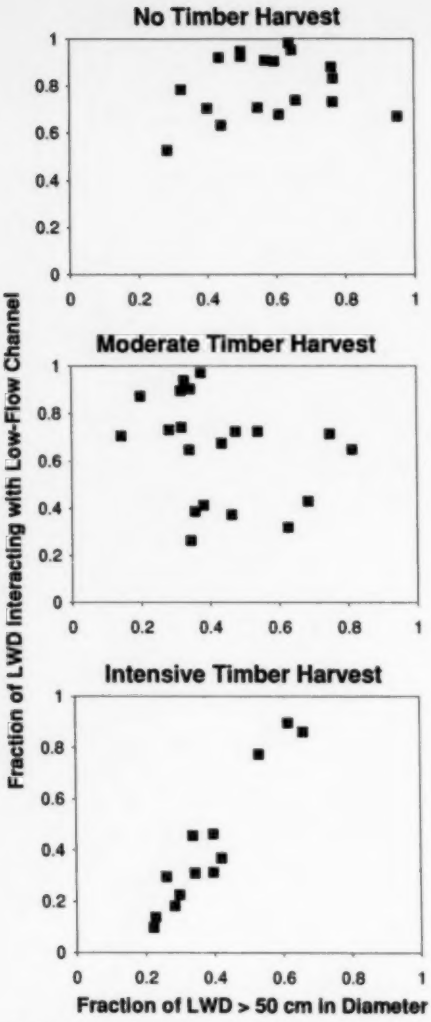

FIG. 8. Fraction of LWD interacting with low-flow wetted channel versus fraction of LWD >50 cm in diameter by timber harvest intensity. Each point represents one stream segment.

Other workers have noted the importance of the relative position of woody debris within the channel in providing for much of the structural complexity and hydraulic stability of in-stream habitat through storage of bedload and the dissipation of stream power (Keller and Swanson 1979; Hogan 1986; Bisson et al. 1987). Position and size are linked to the processes that shape the character of the channel and are among the most important determinants of debris stability (and hence, habitat stability) within forested streams. LWD of sufficient size and when anchored within the channel resists movement by high-flow events.

In streams from unharvested basins, LWD is more evenly distributed within the channel and contributes to habitat character during periods of reduced discharge. If the woody debris is unstable, suggesting overall channel instability, it will be clumped and distributed towards the channel margins and meander bends generally outside the low-flow wetted width (Bryant 1982; Hogan 1986; Maser et al. 1988).

Reduction of LWD following logging eliminates a portion of the buffering capacity against stormflow hydraulics that it afforded the channel. In the first decade following substantial logging, stream channel geometry must adjust to any altered flow regimes and increased sediment input. Especially in alluviated channels, the subsequent channel widening reduces the capacity of the channel to retain even larger sized wood and further exacerbates the processes and persistence of bank erosion and attendant sediment input (Frissell 1992).

Additional sediment entering the channel compounds the effect by overwhelming the channel's inherent bedload transport capacity. Maser et al. (1988) found that channel width increased by 40%, indicating decreased stability, after salvage logging had occurred on the North Fork Breitenbush in the Oregon Cascades. Bedload stored behind woody debris becomes susceptible to transport, increasing deposition and scour in a downstream direction (Lisle 1987; Hartman and Scrivener 1990; Bilby and Ward 1991). Alluvial stream channels, those containing riffle habitat types used for spawning by salmon and trout, are particularly prone to episodes of scour and fill. But, because of the insidious nature of these events, little telltale evidence of their occurrence is left to alert one to the destabilizing effect on spawning areas. The significance and extent of this recurring disturbance on survival-to-emergence of salmon and trout eggs have not been fully appraised, as few long-term studies to document the spatial and temporal occurrence of this phenomenon have been done (Frissell 1992; Olson-Rutz and Marlow 1992).

In-stream Habitat Area and Character

Intensive harvesting within basins alters the relationship between pools and riffles. These results support the conclusion that forest management affects in-stream habitat complexity by decreasing both pool depth and surface area. In contrast, the greatest within-stream variation, mean depth, and overall range in pool depths were in sites from unharvested basins, indicating a greater natural diversity of pool character than in sites within harvested basins. Frissell (1992) noted the same relationship in his study of moderately and intensively logged coastal streams of Oregon. Deep pools are especially important to adult and juvenile salmonids during drought periods and when ambient stream temperatures are elevated due to riparian canopy removal (Bjornn and Reiser 1991). Their loss suggests a decreased availability of the mosaic of habitats needed to sustain aquatic organisms during times of especially low flow or in areas where water temperatures may be abnormally high. Bisson and Sedell (1984) found that streams in western Washington in which logging debris had been removed had longer riffles and fewer pools than comparable streams within old-growth forested basins and that fish communities showed a narrowed range of age classes. This practice of "woody debris removal" following clear-cut harvesting was vigorously followed during the 1960's and 1970's and often included all LWD found within the channel, not just the new debris associated with the recent harvest.

We believe that reduced overall pool area in streams from harvested basins is a result of the reduction in stable LWD because in most streams <4% in gradient, such material can account for most of the hydraulic obstructions necessary for pool formation. Even 50 yr after logging, Andrus et al. (1988) noted that over 70% of all pools >1 m^3 were formed

by LWD, most of which persisted from preharvest supply. It seems clear that a major effect of the reduction of stable LWD within streams will be a consequent reduction in pool type habitats. The relative increase in riffle habitat area is probably related to an overall increase the input of sediment from up-slope sources and bank erosion.

LWD provides much needed structure to stream channels which in turn promotes habitat heterogeneity. LWD promotes pool formation, provides cover, traps and stores sediments transported from upstream, helps stabilize the channel banks by dissipating erosive stream power during high-flow events, and provides essential winter refugia from high current velocities (Bisson et al. 1987, 1992; Fausch and Northcote 1992). Many streams in second-growth forests have become progressively more debris poor following repeated cycles of logging to the channel's edge (Hicks et al. 1991).

If the process of channel widening occurs in response to human-caused changes in the balance of sediment load and the frequency and duration of flood flows, the locational stability of LWD is also reduced. Once the wood is mobilized by flood flows, it collects in the channel in log jams or along channel margins. The role of LWD to provide habitat structure and buffer the channel banks from the erosive forces of flood flows is reduced or lost.

The consequence for stream fishes can be particularly acute in lower gradient (<2% slope) alluviated reaches traditionally used for spawning by adults and rearing by juveniles. Multiple events of bedload scour and redeposition in a given year can eliminate salmon and trout redds from entire spawning reaches and eliminate microhabitats used by juvenile fishes without leaving any evidence. With overall pool area reduced by the reduction in stable LWD, the character of remaining pool habitats is reduced as pools fill in with bed material, or simply by the ephemeral nature of pools formed by debris pieces that are poorly anchored and subject to transport by even moderate winter flows. Certain life stages of stream salmonids are affected unequally by habitat alterations because of age-dependent habitat requirements (Bisson and Sedell 1984; Bisson et al. 1987). Similar effects on overall aquatic community integrity and persistence are suspected but poorly documented in the Pacific Northwest (Bisson et al. 1992).

Conclusions

We agree with Frissell (1992) that without stratification of sample sites to account for variation in channel and valley geomorphology, detection of ecologically important changes due to land use may be severely limited (see also Hicks et al. 1991). We recommend the use of direct, objective measurements of stream characteristics affecting in-stream conditions rather than relative indices or classifications. Collecting information in the form of continuous variables is also advantageous, as it allows the most flexibility in subsequent data analysis (Conquest et al. 1994). We further discourage the use of a pool-to-riffle ratio as a meaningful measure of the effects of land use on instream habitat. In spite of evidence that pools are altered in harvested systems, this index is difficult to obtain, is not repeatable, is based on subjective classification of channel unit types, and is influenced by channel gradient. Most importantly, it appears to be relatively insensitive to the effects of basin-scale timber harvest. Measures of LWD volume and position are easily measured, objective, repeatable, and appear sensitive to even moderate land use practices.

Our database did not originally contain information that was useful in stratifying the sampled streams in our analysis. The subsequent stratification by channel gradient and basin area taken from topographic maps served to reduce variation imposed by larger scale factors not directly affected by forest harvest activities. Efforts and landscape-scale evaluation of the imprint of forest land management should strive to differentiate between natural variability and management-induced changes to measurable habitat parameters that reflect the causal agents (Bisson et al. 1992). Including direct measures of basin-specific timber management history such as road density, stand age by area, and sediment sources would provide valuable insight into mitigation strategies.

The results of this study argue strongly for a new, more integrated approach to aquatic habitat and adjacent forest land management. Further, they raise questions about the overall effectiveness of (1) past and current timber harvest regulations in protecting the physical and biological integrity of aquatic communities and (2) reliance on monitoring variables that have little relation to the processes that shape channels and in-stream aquatic habitat in a managed landscape. The results further question the wisdom of suggesting that management guidelines which merely provide for woody debris recruitment will adequately replace the functional role that such debris has played in forming habitats important to fish communities. The stability of stream channel – its ability to withstand the channel-altering effects of large storm events — determines what it provides in terms of aquatic habitat. Only by establishing stream channel stability and habitat complexity as an explicit objective can we hope to "manage" forested basins to provide essential habitat and ensure the diversity and stability of aquatic communities.

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Quantitative Use of Stable Carbon Isotope Analysis to Determine the Trophic Base of Invertebrate Communities in a Boreal Forest Lotic System

Michel Junger and Dolors Planas[1]

Centre de géochimie isotopique et de géochronologie (GEOTOP), Université du Québec à Montréal, C.P. 8888, Succ. A, Montréal, QB H3C 3P8, Canada

Junger, M., and D. Planas. 1994. Quantitative use of stable carbon isotope analysis to determine the trophic base of invertebrate communities in a boreal forest lotic system. Can. J. Fish. Aquat. Sci. 51: 52–61.

Stable carbon isotope mixing models were combined with inventories of macroinvertebrate biomass to quantitatively assess the trophic base of three contrasting lotic ecosystems in a boreal forest drainage system in spring/early summer. In a second-order partially shaded stream and in a fourth-order unshaded river, $^{13}C/^{12}C$ ratios of autochthonous and allochthonous food sources were distinct, allowing the use of isotopic mixing equations to calculate the relative contribution of both sources to consumer biomasses. In a small shaded lake outlet, isotopic compositions of autochthonous and allochthonous carbon were similar but distinct from that of lake seston which was relatively ^{13}C depleted. The mixing model for the lake outlet thus discriminated between feeding on lake-derived food and on combined autochthonous and allochthonous food sources. Percent food utilization calculated for each invertebrate taxon by a site-specific mixing equation was weighted by biomass data to define the food bases of primary consumer communities. The food base was clearly dominated by lacustrine inputs (which represented >80% of the total food base) in the lake outlet, by allochthonous inputs (≈75%) in the second-order site, and by autochthonous production (≈60%) in the fourth-order site.

Des modèles de mélange d'isotope du carbone stables ont été combinés à des inventaires de biomasse d'invertébrés afin d'évaluer quantitativement la base trophique de trois écosystèmes lotiques contrastants dans un bassin hydrographique de forêt boréale au printemps et au début de l'été. Dans un cours d'eau partiellement ombragé de deuxième ordre et dans une rivière non ombragée de quatrième ordre, les rapports entre $^{13}C/^{12}C$ des apports autochtones et allochtones étaient distincts, ce qui permet l'utilisation d'équations de mélange isotopique pour calculer la contribution relative des deux sources à la biomasse des consommateurs. Au niveau de l'émissaire d'un petit lac ombragé, les compositions isotopiques du carbone autochtone et allochtone étaient semblables mais distinctes de celles du seston lacustre qui était relativement pauvre en ^{13}C. Le modèle de mélange pour l'émissaire d'un lac fait donc la distinction entre l'alimentation à partir d'aliments dérivés du lac et des sources d'aliments autochtones et allochtones. Le pourcentage d'utilisation des aliments calculé pour chaque taxon d'invertébrés par une équation de mélange propre à un site était pondéré par des données sur la biomasse afin de définir les bases alimentaires des communautés de consommateurs primaires. La base alimentaire était clairement dominée par des apports lacustres (qui représentaient >80 % de la base alimentaire totale) dans l'émissaire, par des rapports allochtones (≈75 %) dans le site de deuxième ordre, et par la production autochtone (≈60 %) dans le site de quatrième ordre.

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Our understanding of carbon/energy flow in lotic food webs is limited by our poor knowledge of benthic invertebrate diets. The trophic base of running-water communities originates from two primary sources, terrestrial (allochthonous) organic carbon and in-stream autotrophic production (autochthonous). The relative importance of these two sources to secondary production is an ecosystem attribute which has never been directly measured. The distinction between autotrophic and heterotrophic ecosystems, based on the (primary) production/respiration (P/R) ratio (Odum 1956), is often used as an index of the relative dependence on food originating from within and outside the stream. However, if one is interested in the origin of animal carbon, such an interpretation of P/R ratios may be "inadequate and misleading" (Rosenfeld and Mackay 1987). The use of P/R ratios disregards animal communities, assuming that streams are quantitatively an algal–bacterial world. Rosenfeld and Mackay (1987) suggested that stable carbon isotope analysis, "the method with the greatest potential for accurately assessing the food base of a stream ecosystem", be used to determine the $P_{\text{AUTOCHTHONOUS}}/P_{\text{ALLOCHTHONOUS}}$ (P = secondary production) ratio, a more direct measure of the relative importance of allochthonous and autochthonous carbon to stream macroinvertebrate communities.

The composition of food actually assimilated during an animal's previous feeding history is reflected in $^{13}C/^{12}C$ ratios, overcoming a shortcoming of gut content analysis (Rounick and Winterbourn 1986; Rosenfeld and Roff 1992; Junger and Planas 1993). In the past decade, carbon isotope analysis has been used to study various lotic food webs

[1]Author to whom correspondence should be addressed.

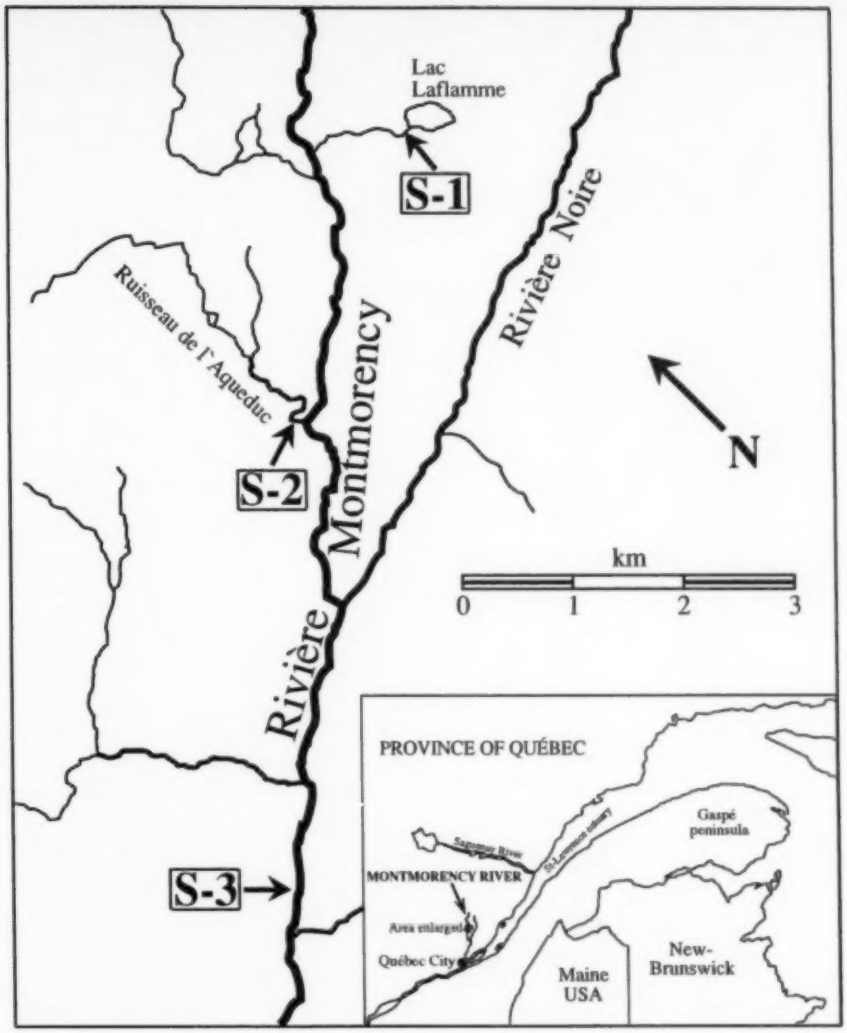

FIG. 1. Locations of the study sites.

(e.g., Winterbourn et al. 1986; Bunn et al. 1989; Rosenfeld and Roff 1992; Forsberg et al. 1993). However, most of these studies were qualitative, and none was an attempt to quantify the overall autochthonous/allochthonous dependence of lotic food webs.

The main objective of our study was to quantitatively estimate the autochthonous/allochthonous dependence of the benthic consumer communities inhabiting three different lotic ecosystems with distinct food sources. We have combined simple two-source mixing models of carbon isotope data with inventories of invertebrate biomasses to calculate the $B_{AUTOCHTHONOUS}/B_{ALLOCHTHONOUS}$ ratio, the biomass (B) analogue of the $P_{AUTOCHTHONOUS}/P_{ALLOCHTHONOUS}$ ratio proposed by Rosenfeld and Mackay (1987).

Study Area

The study was carried out in June 1989, the beginning of the growing season, in three boreal forest streams of different order and degree of shading: first-order Laflamme Creek (site S-1) sampled 75–150 m downstream from the outlet of the small oligothrophic headwater Lake Laflamme, second-order De l'Aqueduc Creek (S-2), and fourth-order Montmorency River (S-3) (Fig. 1). They are located on the Canadian Shield ≈100 km north of Québec City. Morphometric and environmental variables characterizing the study sites are presented in Table 1. At all sites, riparian vegetation consisted of an alder–fir community (*Alnus rugosa* and *Abies balsamea*).

Material and Methods

Standing Stocks

Fifteen replicate samples of stream benthos were taken at each site with a 250 μm − mesh Surber sampler to estimate macroinvertebrate abundances and biomasses. For biomass measures of epilithon (referred to as biofilm), rock scrapings

TABLE 1. Morphometric and environmental variables of sampling sites measured during the study period. Standard deviations for N = 15 are shown in parentheses.

	Laflamme Creek (S-1)	De l'Aqueduc Creek (S-2)	Montmorency River (S-3)
Order	1	2	4
Catchment area (km^2)	0.69	≈6.0	≈265
Altitude (m)	775	597	555
Slope (%)	9.1	3.4	0.9
Width (m)	0.4–1.5	3.6–5.2	54
Mean depth (cm)	17.6 (±6.8)	18.9 (±5.6)	50.4 (±12.0)
Mean current velocity ($m \cdot s^{-1}$)	0.45 (±0.37)	0.55 (±0.27)	0.28 (±0.09)
Discharge ($m^3 \cdot s^{-1}$)	0.01–0.02	0.46	5.9 to >12.1
% shading	90	30	<1
Temperature (°C)	12–15	9–11	13–16.5
pH	6.7–6.9	7.1–7.25	6.9–7.05
Conductivity (μS·cm−1)	28	29	37

were collected following Stockner and Armstrong (1971) on rock surfaces adjacent to each of the 15 Surber samples. Each replicate sample consisted of 30 scrapings for a total surface of 159.3 cm^2. The sites were visited consecutively in the order S-1, S-2, and S-3 between June 13 and 26, 1989. Sampling was carried out systematically at equidistant points along transects: a single longitudinal transect extending over 75 m in narrow S-1, five cross-transects of three samples each in S-2, and a single cross-transect in S-3.

Benthic material from Surber samples was frozen within a few hours. Later, this material was thawed and passed through a 1-mm sieve. The large invertebrate fraction (>1 mm) was sorted, while the smaller material (0.25–1 mm) was preserved in 4% formalin for later analysis. After invertebrates were counted and identified, all taxa were weighed after drying at 60°C until constant weight (48 h) to obtain biomasses. Dry weights may be underestimated because of weight loss due to slow freezing and formalin preservation of invertebrates (Downing 1984). The <1 mm size fraction from S-1, the lake outlet, was processed for only five (randomly chosen) of the 15 replicate samples: invertebrate data are thus presented for a sample size of five in S-1 and 15 in S-2 and S-3.

A subsample of biofilm was filtered on Whatman GF/C filters and then ground for chlorophyll *a* (Chl *a*) determination following Lorenzen (1967). Another was passed through precombusted and preweighed Whatman GF/C filters for biofilm dry weight and ash-free dry weight (AFDW; loss on combustion at 550°C) determination. A subsample was also fixed with Lugol's solution and examined qualitatively for algal species composition.

Stable Isotopes

To determine the isotopic signature of the autochthonous food source, at least four biofilm replicates per site, sampled as described above, were analyzed for isotopic composition. To avoid contamination, invertebrates and debris were carefully removed from biofilm filters.

For the allochthonous signature, alder leaves and fir needles were collected live, decomposing on the forest floor, and from the stream bottom (well-processed litter from the previous fall). For isotopic analysis of dissolved inorganic carbon (DIC) and stream seston, water was sampled at the midpoint of each stream section and at the surface of Lake Laflamme (for seston only). Seston was filtered on precombusted Whatman GF/C filters from which dried particulate matter was subsequently scraped. For isotopic analysis of DIC, stream water was immediately poisoned with $HgCl_2$; within 2 wk, CO_2 was recovered cryogenically after acidification of the samples.

Sorted invertebrates from the 15 replicate samples were pooled by site after drying and weighing. In addition, several of the more abundant large invertebrate taxa were also kept for 2 d in flow-through aquaria to evacuate gut contents. This treatment, however, did not result in the complete clearing of guts, as evidenced by stomachs partly filled, up to about a third in some of the specimens examined. Regression analysis indicated no overall difference of isotopic composition between individual invertebrate taxa that were frozen upon collection and that were kept alive to evacuate their guts: $\delta^{13}C$ (guts evacuated) = $-0.0025 + 0.9948\delta^{13}C$ (nonevacuated), $R^2 = 0.974$, $N = 11$; the slope did not differ significantly from a slope of 1 ($p > 0.9$).

Small formalin-preserved invertebrates underwent two 24-h rinses in distilled water to remove excess formalin. In contrast with Mullin et al. (1984) who found that formalin preservation decreased the $\delta^{13}C$ of marine zooplankton by 2–3‰ after 2 yr in storage, we observed only small (±0.5‰) and inconsistent (mean −0.02‰) effects of formalin on our samples which were held for 2–3 mo (Junger and Planas 1993).

After drying at 60°C, all organic samples were ground to powder and combusted with CuO in vacuum-sealed Pyrex tubes and the evolved CO_2 gas isolated cryogenically and analyzed on a Micromass 602 or a SIRA-12 (both VG Instruments) ratio mass spectrometer. Isotopic composition is expressed as a $\delta^{13}C$ value, defined as the per mil deviation from the standard Peedee Belemnite (PDB limestone) (Craig 1957). Analytical precision of mass spectrometer measurements is ±0.1‰. Isotopic composition of duplicate organic subsamples usually differed by 0.2‰ or less.

To obtain an index of the relative autochthonous/allochthonous trophic dependence of invertebrate primary

TABLE 2. Carbon isotopic composition (as $\delta^{13}C$, ‰) of DIC, primary producers, and stream seston. Apparent isotopic discrimination (D) associated with photosynthesis is shown in parentheses and is reported as $D^{13}C$ (‰) = $\delta^{13}C$(DIC) – $\delta^{13}C$(algal sample).

	S-1	S-2	S-3
DIC	−15.0	−7.2	−7.7
Biofilm samples			
Range	−29.2 to −27.8	−26.7 to 23.6	−24.0 to −21.7
Autochthonous end-member	−27.8	−23.6	−21.7
	(12.8)	(16.4)	(14.0)
Fontinalis sp.	−34.2	−30.2	−25.6
	(19.2)	(23.0)	(17.9)
Stream seston	−28.1	−26.7	−27.4

consumers, $\delta^{13}C$ values characterizing both allochthonous and autochthonous food sources were used as end-members in the following mixing equation:

$$(1)\quad \%\ \text{AUTOCHTHONOUS} = \frac{\delta^{13}C_{\text{sample}} - \delta^{13}C_{\text{allochthonous}} - f}{\delta^{13}C_{\text{autochthonous}} - \delta^{13}C_{\text{allochthonous}}} \times 100$$

where f = +0.8‰, the average ^{13}C enrichment of animal carbon relative to its food (DeNiro and Epstein 1978). This enrichment factor is highly variable, ranging from slightly negative (Macko et al. 1982) to +2.7‰ (DeNiro and Epstein 1978), depending on food source and consumer metabolism.

For each replicate benthic invertebrate sample within a site, the percent dependence on autochthonous primary production for each taxon was weighted by its biomass to obtain values characterizing the benthic community as a whole:

$$(2)\quad \%\ \text{AUTOCHTHONOUS} = \frac{\sum_{i=1}^{x}(\%\ \text{autochthonous}_x \times \text{biomass}_x)}{\sum_{i=1}^{x}\text{biomass}_x}$$

where x represents each taxon. The resulting value was converted to the $B_{\text{AUTOCHTHONOUS}}/B_{\text{ALLOCHTHONOUS}}$ ratio by the following equation:

$$(3)\quad B_{\text{AUT}}/B_{\text{ALL}} = \frac{\%\ \text{AUTOCHTHONOUS}}{100 - \%\ \text{AUTOCHTHONOUS}}.$$

Mean percentage of total invertebrate biomass derived from autochthonous sources was obtained from the distributions of community-weighted values for each replicate of a given site. Error estimates for composite percent autochthonous values thus reflect only biomass composition variability within a site.

Results and Discussion

Epilithic Standing Crop

Mean biofilm Chl *a* standing crops in S-1, S-2, and S-3 were 5.2, 40.2 and 0.9 mg·m^{-2}, respectively. Biomass, measured as either Chl *a* or AFDW, was highest in S-2 and lowest in S-3 ($p < 0.001$, Kruskal–Wallis k-sample test). In S-1 and S-3, the periphytic community consisted mostly of diatoms and secondarily of chlorophytes, with some cyanophytes. In S-2, a red algae, *Batrachospermum* sp., covered over 90% of the bottom surface area with filaments up to 10 cm long during the sampling period.

Benthic Invertebrate Community Structure

Mean total invertebrate biomass was about four times higher in S-1 than in the other two sites: values (±SD) were 3.42 (3.70), 0.78 (0.57), and 0.88 (0.50) g·m^{-2} in S-1, S-2, and S-3, respectively. Dipterans (*Simulium*) dominated biomass in S-1 (Fig. 2), mayflies (*Ephemerella* sp. 2 = *aurivillii* Bengtsson) in S-2 (Fig. 3), and caddisflies (*Hydropsyche*) in S-3 (Fig. 4).[2]

Stable Isotope Analysis of Food Sources

Mean $\delta^{13}C$ of coarse leaf detritus in the streams was −27.4 ± 0.6‰ (SD), not significantly different (t-test, df = 17, $p > 0.1$) from live leaves and needles and forest floor litter material (−27.9 ± 0.8‰). Thus, in-stream microbial decomposition did not seem to alter the overall isotopic composition of allochthonous inputs in our sites. The mean $\delta^{13}C$ of all 19 allochthonous samples was −27.7 ± 0.7‰ (range −27.0 to −29.6‰), the allochthonous end-member value used in the mixing equation established for each site.

The $\delta^{13}C$ of DIC and of autochthonous autotroph samples are presented in Table 2. Whereas the isotopic composition of DIC in S-2 and S-3 indicates that it originated from atmospheric CO_2 ($\delta^{13}C$ = −7 to −8‰; Keeling et al. 1979), the value for S-1 was depleted by more than 7‰. This reflects a sizeable input of isotopically light biogenic (respiratory) carbon from the lake. The inorganic carbon pool in small lakes dominated by allochthonous inputs of organic matter is often ^{13}C depleted because most of it is derived from lake respiration (Oana and Deevey 1960). This appears to be the case for small, shallow Lake Laflamme in which groundwater inputs dominate (Papineau 1989) and large quantities of terrestrial detritus accumulate and decompose.

The $\delta^{13}C$ of biofilm samples were 1.4, 3.1, and 2.3‰ for S-1, S-2, and S-3, respectively (Table 2). Reflecting the isotopic composition of inorganic carbon available to primary producers, the biofilm in S-1 was ^{13}C depleted relative to the higher order sites, as Kline et al. (1990) reported for

[2]Complete data on invertebrate community composition and feeding guilds are available, for a nominal fee, from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council of Canada, Ottawa, ON K1A 0R6, Canada.

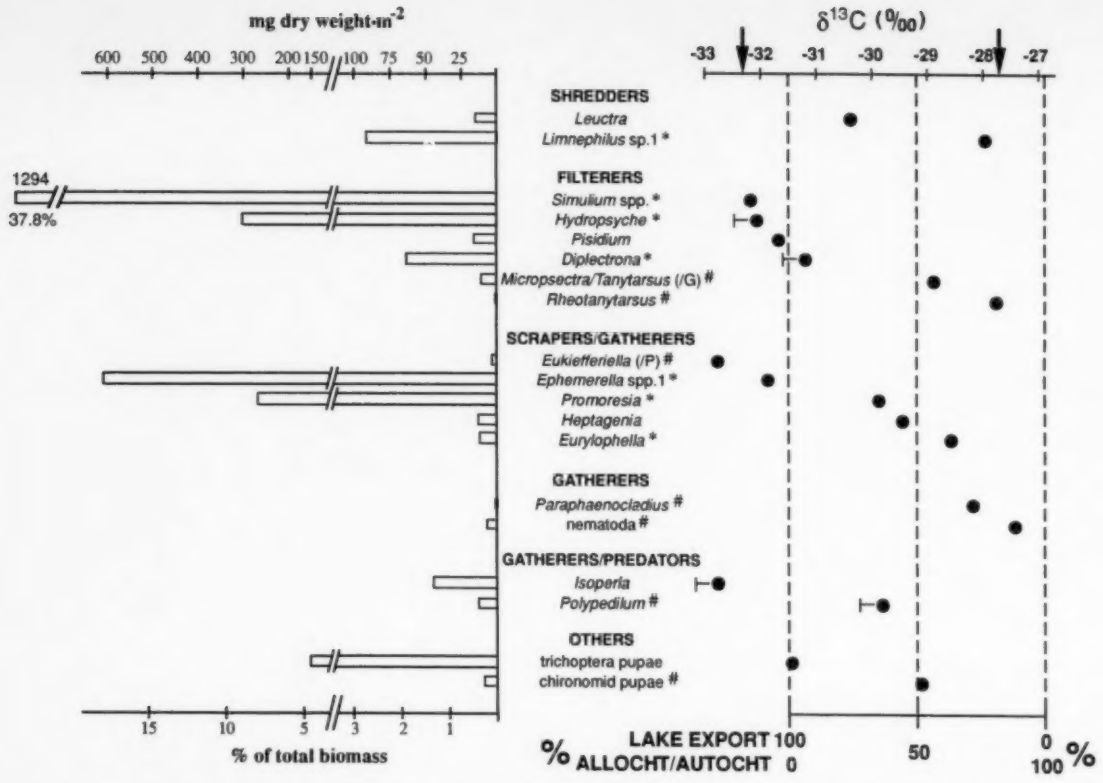

FIG. 2. Left: mean biomass composition of the primary consumer community in Laflamme Creek (S-1), with taxa ordered according to their assignment to functional feeding groups in Merritt and Cummins (1984). Right: carbon isotopic composition of invertebrate taxa. Arrows on the upper axis indicate food source end-members: lake seston at the left and combined autochthonous/allochthonous food sources at the right. The lower axis represents the relative percent contribution of both end-members to invertebrate biomasses. Uppercase letter in parentheses denotes additional classification of a taxon as either collector/gatherer (/G) or predator (/P). Taxa known to be partly carnivorous are shown with a bar at the left corresponding to percent food source dependence assuming 50% predation/50% primary consumption (trophic enrichment of 1.2‰). (There are three types of invertebrate samples: *samples frozen after gut clearing treatment; #samples frozen, thawed, and then preserved in formalin; unmarked taxa frozen shortly after collection.)

an Alaskan lake outlet relative to sites further downstream. In spite of similar isotopic composition of DIC in the second- and fourth-order sites, biofilm was generally more ^{13}C enriched in S-3 than in S-2. The apparent photosynthetic discrimination ($D^{13}C$, sensu Petersen and Fry 1987) against the heavy isotope (Table 2) calculated for the end-member biofilm sample ranged from 12.8‰ (S-1) to 16.4‰ (S-2).

The bryophyte *Fontinalis* was the dominant primary producer in S-1 (671.9 ± 1322.0 (SD) mg AFDW·m^{-2}). It was also present, but much less abundant, in the other sites. Its isotopic composition was always the most depleted of autochthonous samples for a given site (Table 2). Data reported by Winterbourn et al. (1986) and Bunn et al. (1989) also indicate that aquatic moss fractionates inorganic carbon to a greater extent than does algae.

If *Fontinalis* were consumed by invertebrates, it would represent a third isotopically distinct food source and introduce ambiguity in our application of a mixing model. However, it is generally accepted that live aquatic moss is little used as food by stream animals (Hynes 1970), although Jones (1950), Chapman and Demory (1963), Williams and Williams (1979), and Willoughby and Mappin (1988) have reported some ingestion of moss fragments by certain invertebrates. Low $\delta^{13}C$ (Fig. 2) of the three taxa dominating biomass in S-1, *Simulium* spp., *Hydropsyche*, and *Ephemerella* spp. 1 (*dorothea/invaria/rotunda*), could have resulted from assimilation of bryophyte carbon. However, microscopic examination of gut contents indicated that identifiable moss fragments were absent in most specimens examined and never represented more than 5% of an animal's stomach contents (by slide surface area). Thus, in spite of its large standing stock in S-1, aquatic moss did not seem to be eaten by consumers, at least early in the growing season.

Because of the difficulty in completely separating allochthonous debris and microbes assimilating allochthonous carbon from autotrophic periphyton, biofilm samples did not represent pure algal material. The autochthonous end-member was therefore established as the $\delta^{13}C$ value of the biofilm sample with the "cleanest" algal community for each site (Table 2). Microscopic examination indicated that algal cells made up >90% (by slide surface area) of these samples in S-1 and S-2, while recognizable algae repre-

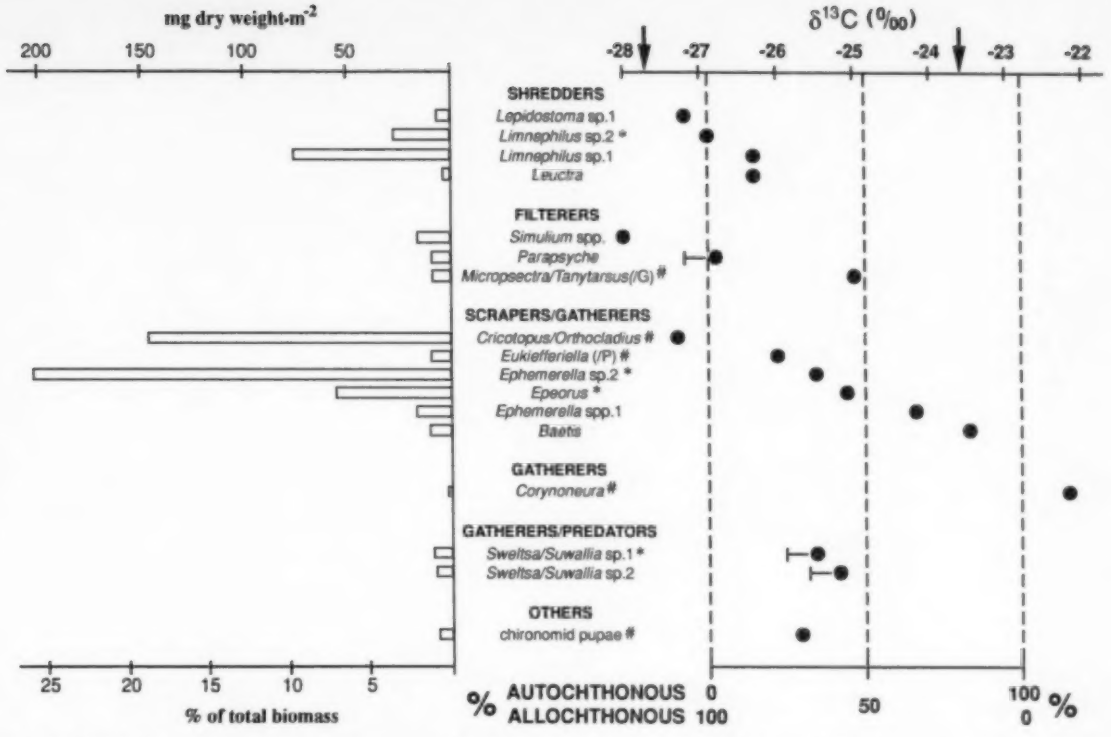

FIG. 3. As for Fig. 2, but for primary consumers in De l'Aqueduc Creek (S-2). In this case, arrows represent the allochthonous (left) and the autochthonous (right) end-members.

sented only 40–50% of the S-3 sample. These "cleanest" algal samples always yielded the most enriched δ^{13}C of biofilm samples from a given site.

Isotopic composition of the autochthonous end-member biofilm sample in both S-2 and S-3 (Table 2) was distinct from the allochthonous value of −27.7‰, allowing mixing equations to be established with ranges between end-members of 4.1 and 6.0‰, respectively. In these two sites, and presumably in other strictly lotic sites in the region, autochthonous food sources were isotopically enriched relative to allochthonous inputs, similar to the findings of Winterbourn et al. (1986), Bunn et al. (1989), and Kline et al. (1990) but in contrast with other observations (Winterbourn et al. 1984; Rounick and Hicks 1985; Rosenfeld and Roff 1992). These studies and ours reveal that carbon isotopic variability of lotic autotrophs is high, both within and among ecosystems, and is determined both by geological and hydrological control of the inorganic carbon source and by differences in photosynthetic isotope discrimination. The latter may be species specific; results for monospecific autotrophic samples (tufts) suggest that it is greater in bryophytes and cyanophytes than in diatoms (biofilm) and chlorophytes (Junger 1992).

Because isotope ratios of both food types coincided in S-1, it was impossible to develop an autochthonous/allochthonous mixing equation for this site. However, a third source of food is available to the benthos of lake outlets: lake-derived organic matter. Surface seston of Lake Laflamme was depleted by 4.6‰ relative to the other food sources in S-1. We therefore established a mixing equation to calculate the relative contribution to consumer biomasses of lake export (end-member = −32.3‰) and strictly lotic food sources (allochthonous and autochthonous combined: end-member = −27.7‰).

At the midpoint of our longitudinal sampling transect in S-1, the δ^{13}C of suspended organic matter approached that of the combined allochthonous and autochthonous end-member (Table 2). This indicates that the isotopic signature of lake seston was quickly masked (diluted) in the particulate organic matter transported by the outlet stream, representing slightly less than 10% as calculated using the mixing equation (without the trophic enrichment factor).

In S-2, ≈30% of suspended organic matter was calculated to be of autochthonous origin (Table 2), corresponding mostly to *Batrachosperum* fragments transported by the current (M. Junger, personal observation). In contrast, the mixing equation indicated that >90% of the suspended particulate load in the higher order site (S-3) was allochthonous in origin.

Stable Isotope Analysis of Primary Consumers

As our data cover only a short time span early in the growing season, results of this study apply to the invertebrate assemblage present at this time of year. The isotopic composition of invertebrates, however, provides an integrated record of feeding over time periods varying in relation to specific life histories and corresponding to taxon-specific organic carbon turnover times (Fry and Arnold 1982; Tieszen et al. 1983).

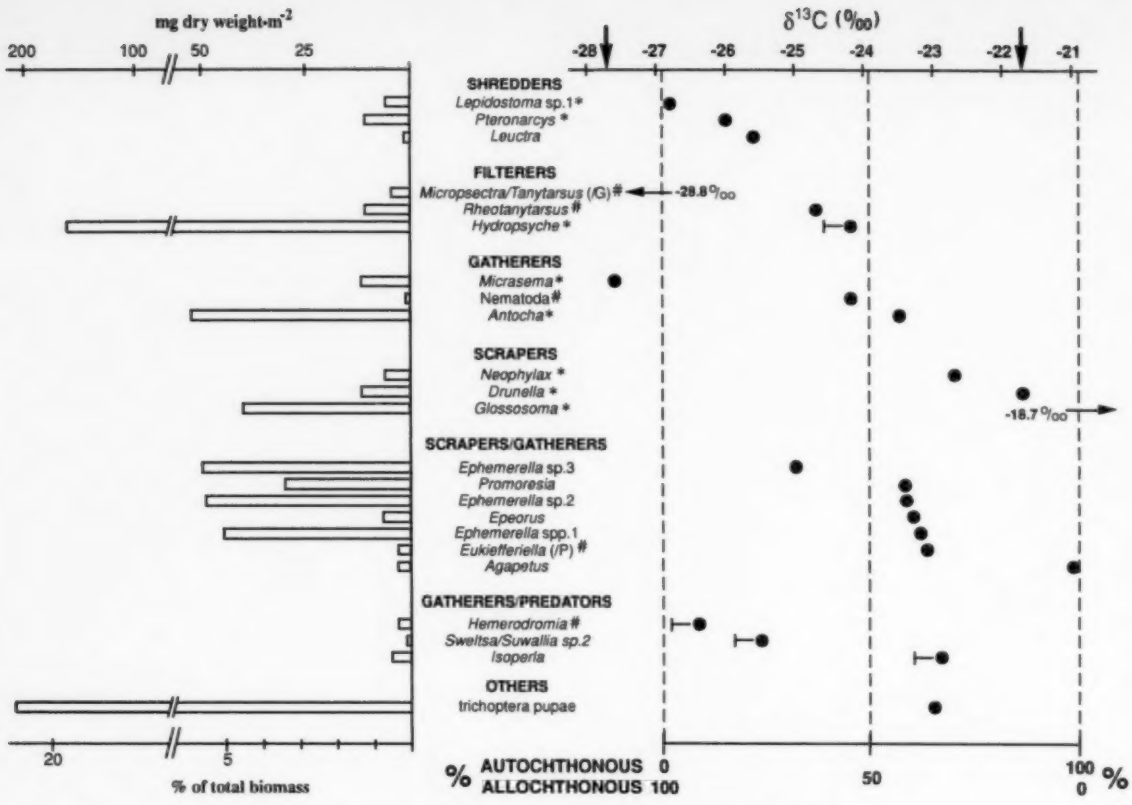

FIG. 4. As for Fig. 3, but for the Montmorency River (S-3).

In general, invertebrate primary consumers in S-1 can be separated into two $\delta^{13}C$ classes (Fig. 2): one ranging from −27.6 to −29.9‰ (≈15–60% lake export) and the other, including black flies and accounting for ≈75% of the total biomass, from −31.1 to −32.8‰ (≈100% lake export). Isotopic composition of most taxa in the latter group was outside the mixing range, probably indicating selective consumption or assimilation of ^{13}C-depleted components of the lake seston or lotic microorganisms growing on depleted lacustrine organic matter.

Filtering invertebrates in S-1, with the exception of the two Tanytarsini chironomids (*Micropsectra/Tanytarsus* and *Rheotanytarsus*), apparently feed almost exclusively on lake seston, as did the dominant mayfly *Ephemerella* spp. 1 (*dorothea/invaria/rotunda*). Settlement of transported lake seston onto the biofilm and in sediment interstices was indirectly evidenced by the fact that the isotopic composition of scrapers and collectors/gatherers was ^{13}C depleted relative to lotic autochthonous and allochthonous sources. Likewise, unless the resident gut microflora (typical of detritivores: Cummins and Klug 1979; Klug and Kotarski 1980) caused a large depletion of the carbon assimilated by *Leuctra*, the isotopic composition of this probably obligate shredder suggested that lacustrine organic carbon may have been associated with coarse detritus surfaces.

All but one (*Diplectrona*) of the eight primary consumer taxa showing >90% dependence on lake export in S-1 were represented in at least one of the other sites. They are opportunist feeders, shifting their diet almost completely toward lake-derived food resources. Some direct or indirect feeding on lacustrine food sources was also evident for all taxa of the more ^{13}C-enriched group (15–60% lake export dependence) in S-1.

The $\delta^{13}C$ values of invertebrates in S-2 (Fig. 3) spanned the whole range of the mixing equation, from black flies (>100% allochthonous) to the chironomid *Corynoneura* (>100% autochthonous). Only three taxa accounting for less than 5% of the total biomass were more than 50% herbivorous. The two dominant taxa in S-2, *Ephemerella* sp. 2 (*aurivillii*) and *Cricotopus/Orthocladius*, both scrapers/gatherers, were calculated to have derived ≈66 and >100%, respectively, of their biomass from allochthonous food sources. The latter taxon, the dominant chironomid in S-2, thus did not feed on *Batrachosperum* filaments among which it was very abundant, but probably collected fine allochthonous particles trapped by the filtering effect of the algal filaments. In contrast, the other, but much less abundant Orthocladiinae, *Corynoneura*, appeared to exploit either the large standing crop of *Batrachosperum* or other periphytic algae. The depleted $\delta^{13}C$, falling outside the mixing range in Fig. 3, of black fly larvae, and to a lesser extent of *Cricotopus/Orthocladius*, suggests that they selectively assimilated an isotopically light component of allochthonous detritus.

Invertebrates from S-3 displayed a relatively large isotopic composition range of 10‰, but only three taxa of the 31 analyzed were outside the bounds of the mixing equa-

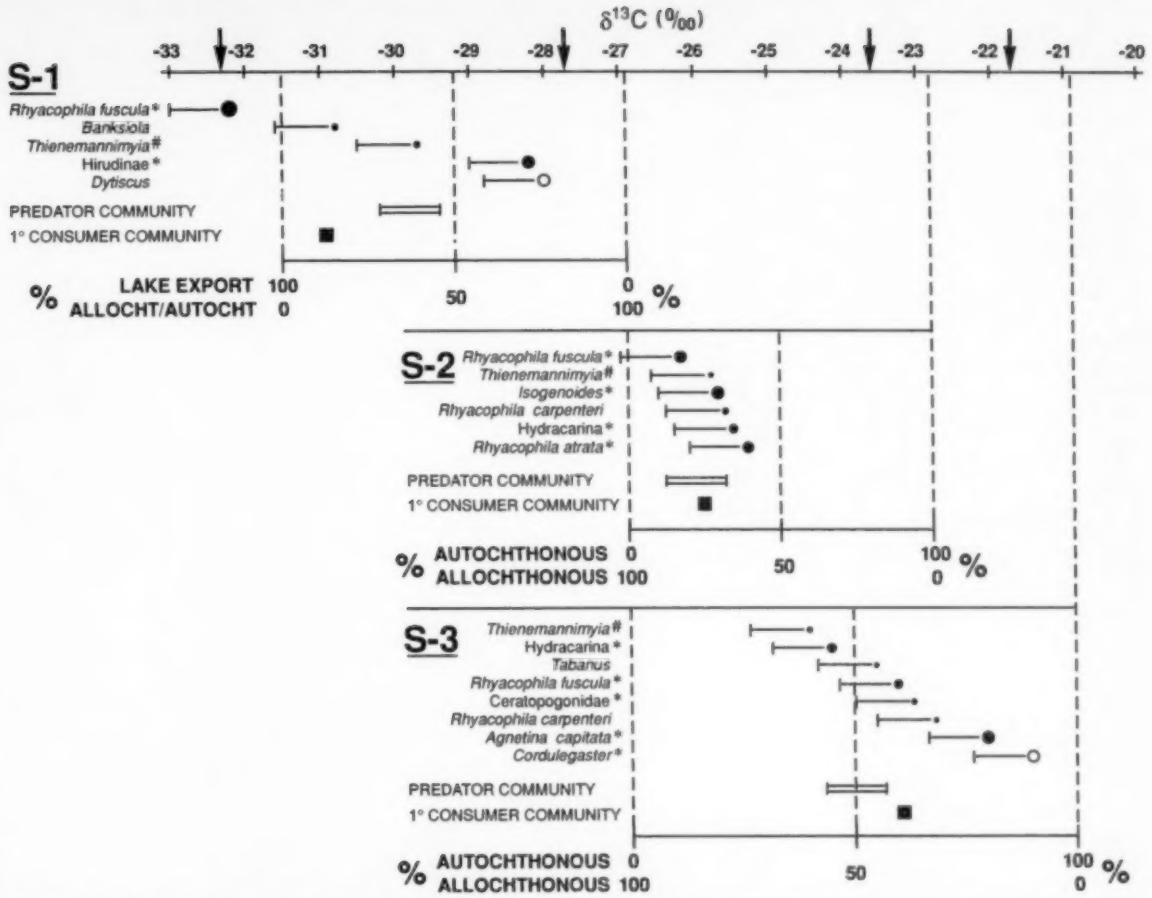

FIG. 5. Carbon isotopic composition (upper axis) and corresponding percent primary food source dependence (lower axes) of predators in all sites. Black circles (whose area is proportional to biomass ranging from 4 to 80 mg·m^{-2}) correspond to measured $\delta^{13}C$ and percent feeding assuming predators behaved as primary consumers with a single trophic fractionation (f) of +0.8‰. The bar to the left indicates the value corresponding to 100% predation on primary consumer prey (f = +1.6‰ relative to primary food sources). Open circles represent taxa present but not collected in standing stock sampling. Black squares are the mean biomass-weighted composite percent food dependence values for the entire primary consumer community, while double lines show the range of values for the predator community assuming an f of +1.6 and +0.8‰, from left to right.

tion (Fig. 4 and 5). The taxa were more evenly distributed over the whole mixing range in this site than in S-2, with 11 primary consumer taxa <50% autochthonous and 12 >50% (Fig. 4). This indicates both a greater importance of herbivory and a higher feeding diversity in the higher order site. Calculation for the dominant taxon, net-spinning *Hydropsyche* larvae, gave ≈45% autochthonous; this value is probably an overestimate, as it partly reflects the double trophic ^{13}C enrichment of feeding on captured drifting invertebrate prey which can represent a considerable portion of this genus' diet (Grafius and Anderson 1972; Benke and Wallace 1980; Parker and Voshell 1983). The isotopic composition of the caddisfly *Glossosoma* was the most enriched of all organic samples (−18.7‰). This may result from selective feeding on an isotopically heavy component of the periphyton by this scraper.

Stable Isotope Analysis of Predators

Predators feeding on primary consumer prey undergo a double trophic enrichment (f) of carbon isotope with regard to primary food sources. However, most predators depend to varying extents on animal tissue and complete their diets with primary food sources including the digestive tract contents of their prey. Percent lake export and percent autochthonous trophic dependencies of invertebrate taxa classified as exclusive predators were thus bracketed by the values calculated using a single f (+0.8‰) and a double f of +1.6‰ (Fig. 5). We did not consider the cause of predators feeding at a higher trophic level on other predators, which would cause their food dependence to shift a further 0.8‰ to the left in Fig. 5.

The $\delta^{13}C$ values of the four predators in S-1 were evenly spread over a range of 20–40 to >100% lake export (Fig. 5), indicating a variety of diets. In contrast, predators in S-2 showed isotope ratios grouped within a narrow range of −26.2 to −25.3‰ (a difference of 22% autochthonous). In S-3, predator isotopic compositions were evenly spread over a broader range (−24.5 to −21.5‰, spanning 50% autochtho-

nous) than in S-2 (Fig. 5), reflecting the more diversified trophic base of the prey community in the higher order site.

Composite Measures of Food Utilization

Biomass-weighted taxon-specific percent food utilizations (percent lake export in S-1 and percent autochthonous in S-2 and S-3) were summed for the total primary consumer community (Fig. 5). Ranges of food dependence values for exclusively predator taxa (Fig. 5) were summed separately to estimate the food base of the predator community. We hypothesized that the allochthonous/autochthonous balance of the primary consumer community would be reflected in the biomass-weighted percent autochthonous range of predators as a whole.

Weighting percent lake export values by the biomass distribution of taxa in S-1, we obtain a mean (±SD) dependence of the total primary consumer community on food derived from the lake of 86.7 ± 12.1% (Fig. 5), although predators ultimately depended ≈10–30% less on organic carbon originating from the lake than did the primary consumer community. Our data for S-1 demonstrate the overwhelming impact of high nutritional quality lake seston on the invertebrate community inhabiting a lake outlet (see review by Richardson and Mackay 1991). S-1 supported the highest biomass of each of the five main insect orders (Junger 1992), and isotopic composition of the dominant taxa indicates their almost exclusive dependence on carbon inputs from the lake. Similarly, Kline et al. (1990) observed that isotopically light invertebrates and salmon in an Alaskan lake outlet reflected dominance of the food web by lake-derived carbon. The trophic importance of lacustrine particulate matter in S-1 was disproportionate to the small fraction of stream transport it represented. Our finding that less than 10% of stream seston sampled 110–120 m below the lake is of lacustrine origin compares well with the calculations of Morin et al. (1988) indicating that black fly larvae ingested 0.8–1.4% of the seston per linear metre of stream in the first 40 m of an outlet stream similar to ours.

Nearly a quarter (23.9 ± 9.2% (SD); $B_{AUTOCHTHONOUS}/B_{ALLOCHTHONOUS} = 0.31$) of total primary consumer biomass in S-2 was derived from autochthonous food sources (Fig. 5). Thus, the very large algal (*Batrachospermum*) standing crop in S-2 did not appear to have been exploited to any great extent by consumers. In fact, the absence of dominant herbivorous invertebrates in this site may have permitted the proliferation of *Batrachospermum* which has been reported to be consumed by several insect larvae (Jones 1950) and by snails (Steinman et al. 1991). The weighted predator percent autochthonous values from S-2 (12–32%) bracketed the primary consumer community value (Fig. 5), suggesting that predators as a whole were not selective in their choice of prey.

In S-3, autochthonous food sources accounted for 60.9 ± 7.0% (SD) ($B_{AUTOCHTHONOUS}/B_{ALLOCHTHONOUS} = 1.56$) of total primary consumer biomass and for 44–57% of predator community biomass (Fig. 5). In contrast with S-2, S-3 displayed an unexpectedly low standing crop of periphyton and a consumer community supported predominantly by autochthonous food sources. Together, these two observations strongly suggest that periphytic biomass in this site was controlled by grazers. The mean Chl *a*/phaeopigment ratio was significantly lower (by 40–45%) in S-3 than in the other sites (Junger 1992). As chlorophyll from ingested algae is rapidly degraded to phaeoborbide and passes unassimilated through invertebrate guts (Cowan and Peckarski 1990), the proportionally high phaeopigment levels in the biofilm may reflect fecal material from intensely grazing larvae rather than senescent algae. This interpretation is supported by the enriched $\delta^{13}C$ value of the end-member epilithic sample from S-3 (Table 2), which indicated that the biofilm was dominated by autochthonous material in spite of the fact that only about 40–50% of it was recognizable as algal cells in microscope examination, with the remainder being amorphous detritus. The isotope data for consumers and biofilm samples thus yielded a consistent picture of the intimate coupling of autotrophic and herbivorous processes in the Montmorency River.

Acknowledgements

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Mitochondrial DNA and Conservation of an Aboriginal Arctic Char (*Salvelinus alpinus oquassa*) from Floods Pond, Maine

Irv Kornfield

Department of Zoology and Center for Marine Studies, University of Maine, 5751 Murray Hall, Orono, ME 04469-5751, USA

and Frederick W. Kircheis

Marine Department of Inland Fisheries and Wildlife, 650 State Street, Bangor, ME 04401-5654, USA

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Periods of low water in Floods Pond, Maine, USA, during spawning seasons for an endemic population of landlocked Arctic char, *Salvelinus alpinus oquassa*, have contributed to several year-class failures. To determine the genetic uniqueness of these fish, samples of Arctic char from five isolated lakes in New England and eastern Canada were examined by restriction endonuclease analysis of mitochondrial DNA (mtDNA) and compared with samples of lake trout (*Salvelinus namaycush*) and Arctic char from Scandinavia. Results suggest that (1) Arctic char of eastern North America should all be considered members of *Salvelinus alpinus oquassa*, (2) char from Floods Pond possess a unique mtDNA banding pattern for one restriction enzyme not observed in fish from any other sampled locality (this difference delineates a distinct lineage of Arctic char whose preservation is warranted on genetic grounds), and (3) unique banding patterns did not characterize any other studied char population, including geographic variants (these populations may be viewed as genetically homogeneous, and none warrant individual protection based upon our genetic characterizations). We contend that genetically identified lineages in the early stages of divergence warrant preservation.

Les périodes de basses eaux dans le lac Floods Pond (Maine, États-Unis) pendant les saisons de ponte d'une population endémique d'ombles chevaliers confinés en eau douce (*Salvelinus alpinus oquassa*) ont joué un rôle dans plusieurs échecs des classes annuelles. Pour déterminer le caractère génétiquement distinct de ces poissons, nous avons examiné des échantillons d'ombles chevaliers provenant de cinq lacs isolés de Nouvelle-Angleterre et de l'est du Canada en effectuant une analyse de l'ADN mitochondrial par l'endonucléase de restriction, et nous avons comparé les résultats à ceux obtenus sur des échantillons de touladi (*Salvelinus namaycush*) et d'omble chevalier de Scandinavie. Les résultats permettent d'émettre les opinions suivantes : 1) les ombles chevaliers de l'est de l'Amérique du Nord doivent être tous considérés comme des membres de la sous-espèce *Salvelinus alpinus oquassa*, 2) les ombles de Floods Pond possèdent un spectre de bandes de l'ADN mitochondrial tout à fait particulier pour une enzyme de restriction qui n'a pas été observée chez des poissons provenant d'un autre endroit échantillonné (cette différence fait apparaître une lignée distincte d'omble chevalier dont la préservation se justifie pour des raisons d'ordre génétique et 3) les spectres de bandes n'ont pas permis de différencier les autres populations d'ombles étudiées, même dans le cas des variantes géographiques (on peut considérer que ces populations sont génétiquement homogènes, et qu'aucune ne justifie une protection individuelle basée sur des caractéristiques génétiques). Nous soutenons que des lignages génétiquement identifiés qui se trouvent dans les premiers stades de divergence méritent d'être préservés.

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The Arctic char[1], *Salvelinus alpinus*, is a taxonomically complex group of salmonid fishes widely distributed around the world at high northern latitudes. Populations in several places over the range of the species possess distinctive morphologies that distinguish them from other local char. In the eastern and southern areas of North American char distribution, there are 11 waters in Maine, USA (Kircheis 1980, 1986), three in New Brunswick, Canada (W. Hooper, New Brunswick Department of Natural Resources, Fredericton, N.B., personal communication), and approximately 100 in southeast Quebec, Canada (Dumont 1982), that have natural populations of landlocked Arctic char.

Of particular interest are the silver char[2] of Floods Pond, Maine, a natural population of landlocked fish character-

[1]We cannot agree upon the appropriate spelling of "char(r)". The American Fisheries Society (Robins et al. 1991) prefers "char" whereas several major texts on this taxon use "charr" (Balon 1980; Johnson and Burns 1984; Kawanabe et al. 1989). Many Scandanavian authors, who for many years preferred "char", are now using "charr" (Anonymous 1992). The International Society of Arctic Char Fanatics (ISACF) allows both "char" and "charr" in its proceedings but objects to using both spellings in the same paper (Hammar 1985). The subject has been reviewed by Morton (1955).

[2]Silver char is used as the common name for these fish instead of the former "Sunapee char". We have shown the Floods Pond char to be distinct from the Sunapee Lake char (F.W. Kircheis, I. Kornfield, and S. Seyoum, unpublished data). Local anglers have long referred to the Floods Pond char as "silver trout".

TABLE 1. Collection localities for samples of fish used in mtDNA comparisons.

Taxon and locality	Sample size	Latitude	Longitude
S. alpinus oquassa			
Big Reed Pond, Maine, USA	10	46°21′N	69°03′W
Floods Pond, Maine, USA	30	44°43′N	68°28′W
Gardiner Lake, Maine, USA	17	46°58′N	68°53′W
Lac Godin, Quebec, Canada	18	47°57′N	71°20′W
Walton Lake, New Brunswick, Canada	20	45°30′N	65°20′W
S. alpinus alpinus			
Jonsvann, Norway	30	63°22′N	10°37′W
S. namaycush			
Clearwater Lake, Manitoba, Canada	3	54°30′N	101°00′W

ized by unique breeding color (Kircheis 1989). Like much of the Arctic char species complex (Behnke 1984, 1989), the taxonomic status of the Floods Pond fish has been the subject of considerable unresolved debate.

Several genetic studies have been conducted to clarify the systematics of Arctic char populations by conventional electrophoretic analysis (Kornfield et al. 1981; Andersson et al. 1983; Magnusson and Ferguson 1987; Partington and Mills 1988). Allozyme studies have been able to differentiate subspecies of char but have provided no information on differentiation among populations. Studies of *Salvelinus* species using restriction analysis of mitochondrial DNA (mtDNA) were conducted by Grewe et al. (1990). In this work, landlocked populations of Arctic char could be clearly distinguished from anadromous populations; comparisons of Arctic char from Great Britain with samples from Floods Pond revealed extremely high similarities. Restriction analysis of ribsomal DNA (Phillips et al. 1992) produced similar results. Thus, while some genetic investigations have convincingly demonstrated genetic isolation of sympatric morphs, the status of allopatric populations, such as the char of Floods Pond, has not been resolved.

Floods Pond is a 260-ha, 50-m-deep oligotrophic lake located in central Maine. Floods Pond contains a native, relict population of landlocked Arctic char and serves as the sole water source for the City of Bangor, Maine, and seven neighboring communities. A total of 54 000 people depend upon the pond for their water, and in 1992, approximately 22.2 million L per day was used. Past water use demands have contributed to periodic lowering of water levels. Three times in the past 10 yr, there was little or no char reproduction in Floods Pond because of exposure of the spawning site, a single 0.3-ha bed of glacial cobble located in shallow water. In addition, in 5 yr during the same 10-yr period, low water levels reduced the size of the spawning area, potentially limiting char reproduction.

Future demands for water could impact the breeding habitat of the silver char in Floods Pond. In 1989, the legislature of the State of Maine directed the Bangor Water District and the Maine Department of Inland Fisheries and Wildlife to cooperate in the development of a management plan that would ensure long-term survival of the silver char while continuing to allow use of Floods Pond as a public water supply. In response to this charge, it was important to clarify the taxonomic status of this fish. The principal goal of our study was to investigate the genetic distinctiveness of the char from Floods Pond to resolve their formal taxonomic status and provide information critical for long-term conservation and management. This was conducted at two levels: (1) comparison with other landlocked populations in eastern North America and (2) comparison with a European char population in Norway. Furthermore, to place these results in the proper context, comparison of Arctic char with lake trout, *Salvelinus namaycush*, was also conducted. We here report the results of these comparisons and consider them within a conservation context.

Materials and Methods

Tissue samples were obtained from fish collected from five Arctic char populations in eastern North America: blueback char (Big Reed Pond, Gardner Lake, Maine, and Walton Lake, New Brunswick), silver char (Floods Pond), and Quebec red char (Lac Godin, Quebec). On the basis of traditional taxonomy, fish from this New England/eastern Canada region are all considered to represent the Arctic char subspecies *Salvelinus alpinus oquassa* (Behnke 1989). Samples of *S. alpinus alpinus*, the western European subspecies, were obtained from a landlocked population in Norway. Samples of lake trout, a species that is closely related to but distinct from Arctic char, were obtained from a State of Maine fish hatchery (Table 1).

Tissues from all specimens were dissected from freshly killed fish and transported frozen on dry ice or liquid nitrogen to the University of Maine. Specimens were kept frozen at −80°C for up to 4 mo prior to processing.

mtDNA was extracted from liver and egg tissues by standard protocols and purified by cesium chloride ultracentrifugation (Lansman et al. 1981; Dowling et al. 1990). Purified samples were dialyzed and stored in an ultracold freezer prior to use. Aliquots of purified mtDNA were digested with a battery of 18 informative restriction endonucleases (Kornfield and Bogdanowicz 1987). Many of these enzymes had recognition sequences of four base pairs (bp) which resulted in the production of a large number of cleavage fragments: *Alu*I (recognition sequence, bp, 4), *Ava*I (4.6), *Ava*II (4.6), *Bst*EII (6), *Cfo* (4), *Dde*I (4), *Eco*RII (4.6), *Hae*III (4), *Hin*cII (5.3), *Hin*fI (4), *Mbo*I (4), *Msp*I (4), *Nci*I (4.6), *Nco*I (6), *Rsa*I (4), *Sau*96I (4), *Sty*I (5.3), and *Taq*I (4). Resulting restriction fragments were end-labeled with

TABLE 2. mtDNA restriction fragment phenotypes observed for all sampled localities. Enzymes composing composite phenotypes are listed (left to right) as in Materials and Methods. *Sty*I (bold) discriminates the Floods Pond population.

Taxon	n[a]	Locality[b]	Composite phenotype
S. alpinus oquassa	22	Floods Pond	**A**AAAAAAAAAAAAAAAA**A**
	8	Big Reed Pond	**A**AAAAAAAAAAAAAAA**CA**
	7	Gardiner Lake	**A**AAAAAAAAAAAAAAA**CA**
	5	Lac Godin	**A**AAAAAAAAAAAAAAA**CA**
	7	Walton Lake	**A**AAAAAAAAAAAAAAA**CA**
	1	Gardiner Lake (1)	**A**AAAAAAAAAD**A**AAAA**CA**
	1	Gardiner Lake (2)	**A**AAAAAAAAB**A**AAAAA**CA**
	1	Gardiner Lake (3)	**A**AAAAAAAAAB**A**AAAA**CA**
S. alpinus alpinus	1	Jonsvann (1)	**B**BAAAAAAAAAAAB**B**B**B**B
	1	Jonsvann (2)	**B**DAAAAAAB**A**AAAB**A**B**B**B
	1	Jonsvann (3)	**B**DAAAAAAAAAC**B**B**A**B**B**
	2	Jonsvann (4)	**B**DAAAAAAAAAAAB**A**B**B**B
	2	Jonsvann (5)	**B**DAAAAAAAAAEC**B**A**B**B**B**
S. namaycush	2	Maine	CCBBBCBBCCCDEACCEC

[a]For restriction enzymes that were polymorphic for eastern North American samples, the number of individuals examined was greater than that indicated for composite phenotypes.

[b]Numbers in parentheses indicate locality-specific variant phenotypes.

TABLE 3. mtDNA restriction phenotypes for *Sty*I (estimated fragment sizes are given in base pairs).

A	B	C	D	E
1736	1565	1736	1736	2192
1565	1474	1565	1565	1314
1474	1314	1474	1474	1048
1314	1212	1314	1314	1003
1003	1003	1003	1003	841
933	742	742	742	796
742	688	688	688	742
688	609	521	562	688
521	521	468	521	562
468	468	410	468	521
358	410	358	358	468
292	358	292	292	358
232	292	232	232	232
	232			

[^{32}P]NTPs and separated by agarose electrophoresis on gels containing molecular weight standards (Maniatias et al. 1982). Restriction banding patterns were visualized by autoradiography. For a number of restriction enzymes, sample sizes were reduced when banding patterns were identical among all North American samples.

Banding patterns were recorded and restriction fragment phenotypes were assigned to all individuals. Intrapopulation variation and interpopulation differentiation in restriction profiles were quantified by standard mathematical procedures (Upholt 1977; Nei and Li 1979; Nei 1987). Fragment data and estimates of sequence divergence were summarized using phenetic (Sneath and Sokal 1973; Rohlf 1988) and maximum-likelihood techniques (Felsenstein 1988, 1989).

Results

A total of 230 cleavage fragments were visualized by digestion with the 18 restriction enzymes. Given an approximate size of 16 800 bp for the mtDNA of *Salvelinus* (Grewe et al. 1990), about 5.9% of the mtDNA genome of these samples was examined. The choice of restriction enzymes used in this study was designed to maximize the detection of differences among char samples; the use of more conservative (six-base) enzymes was limited. The number of bases assayed here was more than four times that in the study of Grewe et al. (1990), thus enhancing sensitivity of the assays.

In all, 13 mtDNA banding patterns or phenotypes were observed among the samples of Arctic char (Table 2). For the North American localities, three of the populations (Big Reed Pond, Lac Godin, and Walton Lake) exhibited a single phenotype that was identical for all individuals; Quebec red char (Lac Godin) had the same phenotype as the blueback char. Fish with this phenotype were common in Gardner Lake. However, this locality also possessed additional banding phenotypes which did not occur in the other samples; three additional phenotypes from Gardner Lake occurred in single individuals and each differed from the common pattern by a single band.

All fish examined from Floods Pond had identical phenotypes that differed from those of all other Arctic char for banding produced by the enzyme *Sty*I (Table 3). This unique pattern, "A", possessed one additional fragment (933 bp) which was not present in the "C" phenotype that was common to all other eastern populations (Fig. 1). The banding phenotypes for Floods Pond char produced by all other restriction enzymes were identical to the common patterns observed in other eastern population samples. Details on restriction fragment patterns for other enzymes may be obtained from the senior author upon request.

Sequence divergence estimates based upon shared banding patterns were calculated for all composite mtDNA phenotypes. Percent nucleotide sequence divergence (p) among phenotypes for char from New England and eastern Canada was very small (p = 0.02–0.12%, mean = 0.07%). Despite having a unique cleavage pattern for *Sty*I, char from Floods Pond exhibited very low sequence divergence with the cleavage phenotype for blueback char and Quebec red char sam-

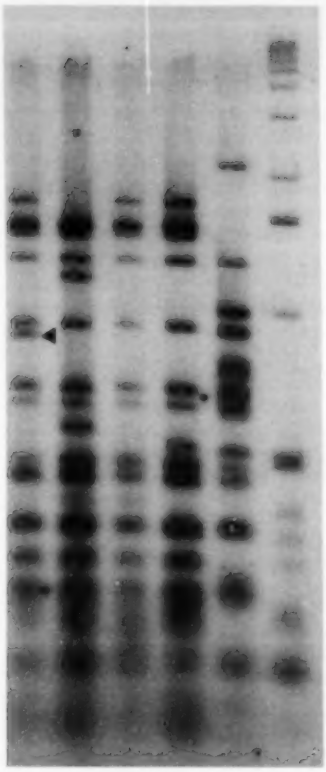

FIG. 1. Autoradiograph of mtDNA char populations digested with the restriction enzyme *Sty*I. Cleavage phenotypes (left to right) are A, B, C, D, and E. Note the band (arrowhead) that is present in "A" but absent from all other patterns. Geographic distribution of banding patterns (phenotypes) is given in Table 3. The banding pattern in the far right lane is a molecular weight size standard (BRL, Bethesda, Md.).

ples (p = 0.03%). By contrast, sequence divergence between the North American subspecies of Arctic char, *S. a. oquassa*, and the Scandinavian subspecies, *S. alpinus alpinus*, was larger (p = 0.42–0.78%, mean = 0.50%). Sequence divergence between Arctic char and lake trout averaged 3.55%.

Relationships among char samples were visualized by clustering the estimates of sequence divergence among mtDNA banding phenotypes (UPGMA; Sneath and Sokal 1973). The resultant phenogram (Fig. 2) depicts the low divergence among eastern North American samples of char. The population from Floods Pond is embedded within a cluster of eastern phenotypes. However, because of the high similarity among these fish, the ordering of groups within this cluster is largely arbitrary. By contrast, these phenotypes were distinct from the samples representing the subspecies from Scandinavia. Finally, all Arctic char are genetically well separated from lake trout. Associations among char mtDNAs were statistically examined by bootstrapping (100 replicates) of banding patterns (Felsenstein 1988). The resulting maximum-likelihood network was similar to the phenogram; the North American phenotypes were significantly separated from the Scandinavian phenotypes (p = 100%, results not shown).

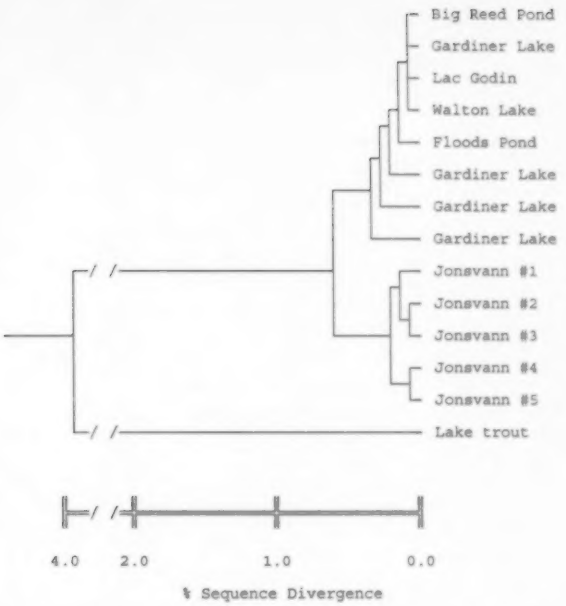

FIG. 2. Relationships among char populatons based on observed mtDNA phenotypes. Clustering was performed on estimates of genetic divergence obtained from mtDNA banding patterns. Cophenetic correlation = 0.997.

Discussion

Systematic Implications

It is clear from the mtDNA analyses conducted here and from the molecular studies of Grewe et al. (1990) and Phillips et al. (1992) that populations of Arctic char from eastern North America are of very recent origin. Given the geological history of the region (Borns 1988), the isolated populations we studied probably originated after glacial withdrawal less than 15 000 yr ago. The results from earlier electrophoretic studies are consistent with this idea (Kornfield et al. 1981; Andersson et al. 1983; Magnusson and Ferguson 1987; Partington and Mills 1988). Because of the many caveats associated with application of a molecular clock to mtDNA (Moritz et al. 1987; Hillis and Moritz 1990; T.E. Dowling, Arizona State University, Tempe, Ariz., personal communications), we will not use it to estimate absolute separation time.

By all characterizations, the samples of char from eastern North America are very closely related. The low levels of estimated sequence divergence and the absence of stable or significant clustering (Fig. 2) are similar to observations made among conspecific populations in a diversity of fishes including other salmonids (see Avise et al. (1987) and Gonzalez-Villasenor and Powers (1990) for reviews). None of the char populations that we studied should be distinguished by subspecific or specific rank. Formal taxonomic status is not warranted for the char of Floods Pond, Maine blueback char, or Quebec red char.

As a group, the fishes from eastern North America are readily distinguishable from the other subspecies in this study represented by specimens of landlocked char from

Norway. The average sequence divergence between char from eastern North America (silver, blueback, and Quebec red) and Norway was $p = 0.50\%$. This level of divergence is consistent with that observed between geographically isolated populations of freshwater fishes, including subspecies (Gonzalez-Villasenor and Powers 1990; Meyer et al. 1990). Grewe et al. (1990) compared mtDNA samples of *S. alpinus oquassa* and *S. alpinus alpinus* (Floods Pond versus Lake Windermere, England) and recorded lower divergence between them ($p = 0.22\%$) than we did. However, their estimate may have been conservative in view of the number of sites assayed. In a maximum-likelihood analysis, samples from the two subspecies formed groups that were statistically distinguishable. The extent and pattern of differentiation between these groups strongly support their recognition as representatives of discrete subspecies.

Despite their overall genetic similarity to neighboring populations, the char of Floods Pond possess a unique mtDNA banding pattern for one restriction enzyme. Our earlier allozyme studies (Kornfield et al. 1981) did not indicate any differences in heterozygosity among populations. By contrast, fixation of a mtDNA variant in the Floods Pond char suggests that the population went through a bottleneck in the past (see Leberg 1992). The difference in the *Sty*I phenotype is equivalent to a change in one base pair among the estimated 1000 bases examined. Simple extrapolation to the entire mtDNA sequence of 16 800 bp suggests the existence of 15 additional base changes. While mtDNA is generally used as a proxy to infer the extent of genetic differences that occur in nuclear DNA, it is not realistic to numerically extrapolate to this class of DNA. Differentiation of mtDNA generally implies parallel differentiation at the nuclear level (Karl and Avise 1992), but mtDNA is a much more sensitive indicator of population size effects.

Quebec red char from Lac Godin and char from Big Reed Pond, Gardner Lake, and Walton Lake had no distinctive mtDNA banding patterns. From the perspective of evolutionary genetics, the apparent absence of DNA phenotypes which could distinguish any of these populations means that there is no compelling reason for preserving the genetic material of any particular lake. That is, it does not matter exactly which populations are conserved as long as the genetic lineage of Arctic char that is common to all of these populations is preserved. By this reasoning, if the mtDNA from Floods Pond char were indistinguishable from that of the other populations, there would be no genetic justification for preservation of the population as distinct from other char in the region. We appreciate the perspective that theoretically all populations should be protected, since they may harbor undiscovered unique differences. Pragmatically, demonstrated uniqueness provides a legitimate basis for advocating conservation of a population. The presence of a mtDNA banding phenotype in all individuals from Floods Pond ($n = 22$) and its absence from all other North American fishes studied ($n = 52$) justifies the conclusion that these fish represent a distinct genetic lineage of North American Arctic char. This lineage is not present in the descendants of char from Sunapee Lake that occur in Idaho (F.W. Kircheis, I. Kornfield, and S. Seyoum, unpublished data). Thus, protecting the Floods Pond *lineage* of Arctic char is warranted on genetic grounds.

We note that conventional methodologies have also consistently demonstrated the uniqueness of the fish from Floods Pond. Waters (1960) determined that the Floods Pond population was significantly different from five blueback char populations based on serological studies and an examination of meristic characters. Qadri (1974), although he considered the Quebec red char *Salvelinus marstoni*, the blueback char, and the Floods Pond char all the same suspecies, found significant differences in the Floods Pond char for 42.8% of the meristic characters he examined. Vladykov (1954) concluded that the Quebec red char and the blueback char were the same subspecies but that the so-called Sunapee char, *Salvelinus aureolus*, was unique. Kendall (1905) felt that the blueback char from Rangeley Lake and Rainbow Lake (Maine) were "quite different" from the silver char of Floods Pond.

Conservation Implications

The challenge of protecting the char from Floods Pond is driven by two competing, but not mutually exclusive, perspectives: the statuatory requirement for preserving the Floods Pond char in its present habitat and the need for a potable water supply for a growing human population. Three approaches are being taken to achieve accommodation. First, consumers are being asked to conserve water and some have been alerted to the possibility that they may have to develop alternative sources of supply. Second, artificial spawning substrates have been recently constructed in Floods Pond; these areas may permit natural reproduction during periods of low water. Finally, silver char have been introduced into a number of waters in Maine (Kircheis 1989). At least one of these introductions, at Long Pond, has resulted in the establishment of a stable, reproducing population. To the degree that Long Pond remains free of introduced competitors and predators, the genetic lineage of silver char is now protected.

A question of more global implication is raised by the results of this study. We found that the silver char in Floods Pond have a unique mtDNA composition which mandates their protection. However, there are other, geographically close char populations that are in little danger and are extremely similar genetically to the silver char. Some feel that protecting this degree of difference does not warrant large amounts of money and possible inconveniences to humans. Consistent with this perspective, Morowitz (1991) suggested that extinction is an inevitable result of human population growth and that if economics is to be used as an argument for protection, then the degree of uniqueness must be considered.

While it may be true that the silver char are only slightly different from other populations, we are the custodians of this difference. If water usage were to have continued without regard for the char, a unique line of genetic diversity might be lost. If this were only a single incident in the region, then consequences would be minimal. But when considered in the context of the extinction of the Monadnock trout in New Hampshire (Kendall 1912), the blueback char of Rangeley, Maine (Kendall 1914), the char of Sunapee Lake (Newall 1958), and unknown and uncounted other "types" of fish, the cumulative impact is substantial. We suggest that the silver char of Floods Pond is an appropriate symbol for preservation.

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Use of Otolith Microchemistry to Discriminate *Oncorhynchus nerka* of Resident and Anadromous Origin[1]

B.E. Rieman and D.L. Myers

USDA Forest Service, Intermountain Research Station, 316 E. Myrtle, Boise, ID 83702, USA

and R.L. Nielsen

Oregon State University, College of Oceanography, Corvallis, OR 97331-5503, USA

Rieman, B.E., D.L. Myers, and R.L. Nielsen. 1994. Use of otolith microchemistry to discriminate *Oncorhynchus nerka* of resident and anadromous origin. Can. J. Fish. Aquat. Sci. 51: 68–77.

We used a wavelength dispersive microprobe to describe patterns in otolith microchemistry of sockeye salmon (*Oncorhynchus nerka*). Patterns in Sr/Ca ratios in transects across otoliths were consistent with changes in environmental chemistry associated with life history. The patterns we observed were consistent with those described for other salmonids. We found that Sr/Ca ratios in otolith primordia of fish of known anadromous origin were significantly higher than those in otolith primordia of fish of known resident origin. However, variation among samples was associated with differences in chemistry of the freshwater environments. These differences could confound attempts to discriminate sympatric resident and anadromous forms in lakes where Sr/Ca ratios are high. Samples used to discriminate origin of emigrants from Redfish Lake, Idaho, confirmed the presence of both resident and anadromous fish, but the two groups were not clearly resolved. Otolith microchemistry has the potential to determine the parental origin of *O. nerka* and to describe life history patterns, but may not clearly identify all individuals in all lakes. More work is needed to determine the inherent variability among individuals and among populations and to determine the influence that migration, spawning, and incubation environments have on the chemistry of otoliths.

Nous avons utilisé une microsonde à dispersion de longueur d'ondes pour décrire les profils de la microchimie des otolithes chez le saumon rouge (*Oncorhynchus nerka*). Les profils des rapports Sr/Ca dans les coupes transversales des otolithes concordaient avec les modifications de la chimie environnementale pendant le cycle vital des poissons. Les profils observés concordaient avec ceux qui ont été décrits pour d'autres salmonidés. Nous avons trouvé que les rapports Sr/Ca dans les primordia des otolithes de poissons dont on connaissait l'origine anadrome étaient nettement plus élevés que chez les poissons connus comme résidents. Toutefois, la variation parmi les échantillons est associée à des différences dans la chimie des milieux dulcicoles. Ces différences pourraient entraver les efforts déployés pour distinguer les formes résidentes et anadromes sympatriques dans les lacs où les rapports Sr/Ca sont élevés. Les échantillons utilisés pour distinguer l'origine des poissons quittant le lac Redfish (Idaho) ont confirmé la présence de résidents et d'anadromes, mais les groupes n'ont pas été clairement séparés. La microchimie des otolithes offre la possibilité de déterminer l'origine parentale de *O. nerka* et de décrire les épisodes de son cycle biologique, mais ne permet pas d'identifier clairement tous les individus dans tous les lacs. Il est nécessaire de poursuivre les travaux pour déterminer la variabilité inhérente entre individus et entre populations, et pour déterminer l'influence qu'ont sur la chimie des otolithes les milieux où ont lieu la migration, la fraye et l'incubation.

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Otolith chemistry has been used to describe the environmental history of individual fish (Gauldie et al. 1980; Kalish 1989; Radtke 1989; Radtke et al. 1990). Using a wavelength dispersive microprobe, Kalish (1990) found patterns in strontium (Sr) and calcium (Ca) content, expressed as the Sr/Ca ratio, across otoliths of brown trout (*Salmo trutta*), Atlantic salmon (*Salmo salar*), and rainbow trout (*Oncorhynchus mykiss*), that were associated with the varied environments and life histories of anadromous and nonandromous forms. Kalish (1989) showed that sea-farmed rainbow trout passed a chemical signal in the form of elevated Sr to the nucleii of the otoliths of their progeny. He concluded that the Sr/Ca ratio in otolith primordia can be used to distinguish the progeny of sympatric anadromous and nonanadromous salmonids.

Discrimination of resident and anadromous forms is potentially useful for the research and management of sockeye salmon (*Oncorhynchus nerka*). Anadromous and resident (kokanee) forms of sockeye salmon commonly occur in sympatry throughout much of the species range (Ricker 1940, 1959; Wood and Foote 1990). The two forms give rise to each other (Ricker 1940, 1959, 1972; Foerster 1947; Rounsefell 1958; Bjornn et al. 1968; Nelson 1968; Scott 1984; Graynoth 1987; Foote et al. 1989), but the impor-

[1]The use of trade or firm names in this paper is for reader information only and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

tance and dynamics of such interaction are unknown. Anadromous sockeye salmon have founded persistent kokanee populations (Ricker 1940; Graynoth 1987), and sustained production of anadromous fish has been established from a kokanee population under artificial circumstances (Kaeriyama et al. 1992). Reproductive isolation and resulting adaptation to the freshwater environment, however, might limit the success of kokanee or hybrid forms that attempt anadromy in the wild (Wood and Foote 1990; Taylor and Foote 1991; Foote et al. 1992).

Anadromous sockeye salmon were once produced in lakes throughout the Snake River Basin in Idaho and Oregon. Although kokanee are still found in a number of these lakes, dams and other barriers have eliminated access for anadromous fish to most. Survival of salmonid smolts in the Snake River Basin has declined substantially with hydropower development (Ebel 1977). Smolt-to-adult survival is probably a limitation for those *O. nerka* populations that still have access to the ocean. An anadromous form of sockeye salmon has persisted only in Redfish Lake in Idaho, and that run is on the verge of extinction (Waples et al. 1991). Kokanee persist in most of these lakes and at least some fish emigrate at the same time and size as typical sockeye smolts (Bjornn et al. 1968; Idaho Department of Fish and Game, Boise, Idaho, unpublished data). Kokanee might maintain or refound the anadromous form in Redfish Lake during or following periods of severe restriction in migrant survival (Bjornn et al. 1968; Waples et al. 1991). Discrimination of origin in *O. nerka* emigrating from and returning as anadromous adults to Redfish and other lakes would be informative. The role that resident fish play in the maintenance or refounding of an anadromous form of sockeye salmon is clearly an important concern for future management and the potential recovery of anadromous stocks throughout the basin.

This study was conducted to determine whether patterns in otolith microchemistry of sockeye salmon are consistent with life histories and with patterns described for other species. Our approach was twofold. First, we obtained otoliths from fish of known or assumed origin (anadromous or resident female parent) from several stocks of *O. nerka*. We used a wavelength dispersive microprobe to determine whether the Sr/Ca patterns in our otoliths were consistent with the varied environments and life histories of resident and anadromous fish. Second, we attempted to discriminate the resident versus anadromous origin of *O. nerka* that emigrated from or returned as anadromous adults to Redfish Lake.

Materials and Methods

Rationale

Our analysis was based on the low-level substitution of Sr for Ca in the aragonite matrix of an otolith during growth (Kalish 1989, 1990). Although the Sr and Ca content in the otolith may be variable (Kalish 1989), Sr/Ca ratios in otoliths and ova reflect the relative amounts of Sr and Ca in the environment (Kalish 1990). In anadromous salmonids vitellogenesis is initiated while the female is still in the ocean. The Sr/Ca ratio of seawater can be much higher than that typically found in freshwaters. Kalish (1990) assumed Sr/Ca ratios of 0.0087 for seawater versus 0.0019 for freshwater on average. He found a corresponding difference in the Sr and Ca content of the ova from nonanadromous and anadromous forms of rainbow trout. The multiple primordia of salmonid otoliths are the first calcified structures to form in the developing embryo and are present at least several weeks prior to hatch. The elemental composition of the primordia that develop directly from the yolk should reflect the elemental composition of that yolk, and ultimately the life history of the female parent. Kalish (1990) found that the chemical composition of sagittal otolith primordia could be used to clearly discriminate individual rainbow trout from female parents held in freshwater or seawater.

Otolith Samples

We obtained otoliths from the progeny of resident and anadromous female parents at Redfish Lake, in Stanley Basin, Idaho (Table 1). A resident stock of kokanee spawns in Fishhook Creek, a tributary to the lake. The Fishhook Creek stock can be distinguished from anadromous fish on the basis of size, and the time and location of spawning. In addition, all anadromous adults were trapped as they attempted to enter the lake in 1991. Therefore, the fish spawning in the lake or in Fishhook Creek had to be fish that matured in the lake. Eggs were collected and fertilized at Fishhook Creek on two occasions in September 1991 as part of an independent research project. Embryos were transported directly to the Idaho Department of Fish and Game Eagle Island Hatchery where they were incubated, hatched, and reared. We sacrificed fish for otolith samples at several times between hatch and yolk absorption. Otolith samples from the Fishhook Creek kokanee population represented six separate female parents. We also collected otoliths from adult *O. nerka* spawning in Fishhook Creek. Although the Fishhook Creek adults could have been residual progeny of anadromous adults, they are reproductively isolated from the anadromous stock. Kokanee spawning in Fishhook Creek spawn at least 1 mo earlier than the known anadromous fish that have only been observed spawning along the lake shore. Because of the isolation from the known anadromous spawning site and time, we assumed that the Fishhook Creek samples represented fish of resident-parent origin.

One female and three male anadromous adult sockeye salmon returned to Redfish Lake in 1991. In October, as part of the endangered species recovery program, the single female was spawned in captivity. Her eggs were fertilized with sperm from each of the three males. The embryos were incubated, hatched, and reared in the same facility, in identical incubation chambers, and with the same water supply as the resident fish. Because of the later spawning time the anadromous origin embryos were brought into the hatchery about 1 mo after those of resident origin. However, because the water source is a well, incubation temperatures did not vary significantly between the two groups. We obtained otoliths only from mortalities that occurred during incubation and rearing. Our samples represented all of the three matings.

We obtained additional samples from *O. nerka* in other lakes (Table 1). We collected otoliths from kokanee in Alturas Lake, about 25 km from Redfish Lake. Although Alturas Lake once supported an anadromous run, anadromous fish no longer have access to the lake and none has returned to the lake in more than 20 yr. The Alturas Lake samples represent samples of resident-parent origin, but from a distinct watershed in the Stanley Basin. The National

TABLE 1. Sources, origin, and number of otoliths used for microchemistry analysis.

	Origin	Number analyzed
Redfish Lake, Idaho		
1991, 1992 adult returns	Anadromous	5
Progeny of adult returns	Anadromous	15
Fishhook Creek adults	Resident	10
Progeny of Fishhook Creek adults	Resident	11
1991 emigrants	Unknown	94
Alturas Lake, Idaho		
Juveniles	Resident	8
Wenatchee Lake, Wash.		
Adults	Anadromous	6
Juveniles	Anadromous	2
Takla Lake, B.C.		
Anadromous adults	Anadromous	4
Residual adults	Anadromous	4
Resident adults	Resident	3

Marine Fisheries Service provided samples of anadromous-origin adults and outmigrating smolts from Wenatchee Lake, tributary to the Columbia River in Washington. Resident-origin fish were not available from Wenatchee Lake. The Canadian Department of Fisheries and Oceans provided samples from anadromous adults and resident adults from Takla Lake in the headwaters of the Fraser River. The parental origin of the Takla Lake fish is not certain, but phenotypic and genetic information was used to characterize the fish as resident, residual (remaining in the lake but originating from an anadromous female parent), or anadromous (C. Foote and C.C. Wood, Department of Fisheries and Oceans, Nanaimo, B.C., personal communication of unpublished data).

Otolith samples of unknown parental origin were available from juvenile fish that emigrated from Redfish Lake in 1991. In May, 861 of an estimated 4500 emigrants were trapped about 0.5 km below the outlet of the lake. Trapping was conducted through the full duration of the migration by the Idaho Department of Fish and Game as part of a captive broodstock development program. The emigrants in our sample ranged from 84 to 115 mm fork length. Because no more than four anadromous adults were believed to have spawned in the lake in 1988 or 1989 (Idaho Department of Fish and Game, Boise, Idaho, unpublished data), we anticipated that resident origin fish contributed to the emigration. Our otolith samples came from fish that died either at the trap site, in transportation, or at the Eagle Island Hatchery captive broodstock site. We also obtained otoliths from the four anadromous adults that returned to Redfish Lake and were spawned in October 1991 and a single anadromous male that returned to the lake in 1992.

All otoliths were stored dry in plastic microcentrifuge vials until preparation for analysis.

Analysis

Otoliths were cleaned in deionized water and dried before mounting. Our initial preparation of otoliths from juvenile fish followed Kalish (1990). The otoliths were mounted sulcus-side-up on glass slides with Crystal Bond 509 (Aremco Products Inc.). We ground the otoliths in the sagittal plane to the approximate level of the primordia with 1200-grit wet–dry sandpaper. The much larger otoliths from adult fish were initially mounted sulcus-side-down and ground in the sagittal plane to a level near the primordia with 600-grit and then with 1200-grit sandpaper to provide a thinner sample with better optical properties. The glue was then heated and the otoliths were turned sulcus-side-up and ground to near the primordia as with the juvenile preparations. We ground all (adult and juvenile) otoliths to the precise level of the central primordia with 5.0-μm paper (Buehler Inc.). We finished samples by hand-polishing on 1.0-μm and then 0.05-μm alumina paste (Buehler Inc.). All samples were washed with deionized water in an ultrasonic cleaner and then photographed at magnifications of 140$\times$ and 280$\times$. Photographs were used to "map" the sample and guide the selection of microprobe sites. Immediately before final analysis, samples were again washed with deionized water, air-dried, and coated with a 200-Å (20 nm) carbon layer for surface conductivity.

Elemental analyses were done with a Cameca SX-50 wavelength dispersive microprobe at Oregon State University. Our analyses followed the general procedures outlined by Toole and Nielsen (1992). We used a 15-kv, 50-nA, 5-μm-diameter electron beam for all of our analyses. Standards for Sr and Ca were strontiantite ($SrCO_3$-USNM R10065) and calcite ($CaCO_3$-USNM 136321). For maximum precision, we used a long counting time (40 s) and analyzed each element simultaneously. We report Sr/Ca ratios as normalized mole fractions (Toole and Nielsen 1992) that are equivalent to the atomic ratios reported by Kalish (1990). One potential problem with otolith analysis is the effect of beam damage (Kalish 1990). Under exposure to the electron beam, carbonate and organic material will break down, changing the composition of the area under the beam. In the case of otoliths, the concentration of Ca and Sr will increase because of the loss of CO_2 and H_2O by volatilization. Our use of long counting times and high beam-currents thus precluded analysis for absolute abundances of the individual elements (Kalish 1990; Toole and Nielsen 1992). The technique developed by Toole and Nielsen (1992) and used in this study is

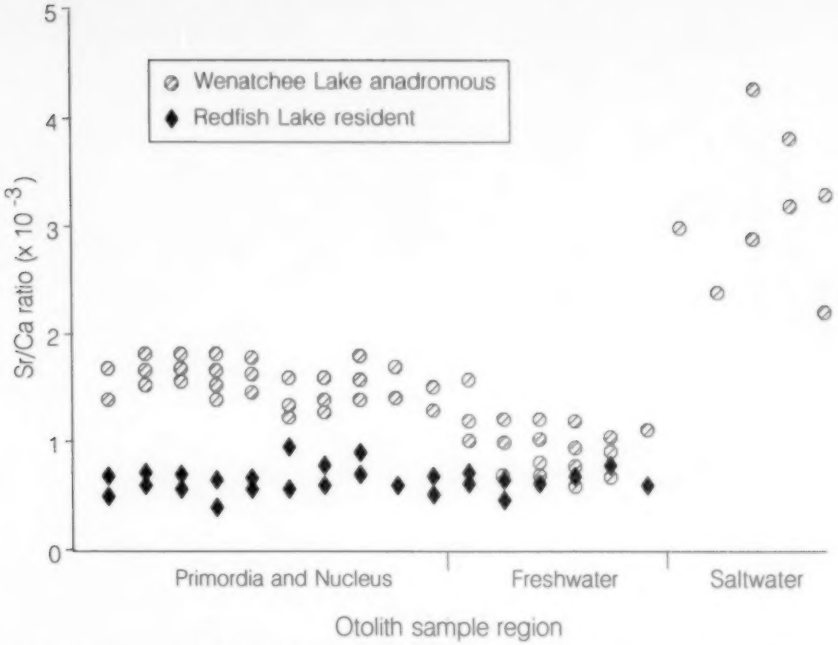

FIG. 1. Elemental Sr/Ca ratios from microprobe transects across three general regions on otoliths from adult resident (Redfish Lake) and anadromous (Wenatchee Lake) *O. nerka*.

based on the assumption that Sr and Ca are equally refractory under exposure to the electron beam. Given that assumption, the ratio of Sr to Ca at the sample site would remain constant throughout the period of beam exposure. To test this assumption, we analyzed a single site on a single otolith repeatedly 10 times. The results (Table 2) show no systematic change in the Sr/Ca ratio. The coefficient of variation (CV), calculated as the $SD_{Sr/Ca}$·Mean Sr/Ca^{-1}, for the 10 samples was about 0.11.

We classified sampling regions on individual otoliths as (1) *primordia* — sites directly in the primordia or in nuclear material immediately adjacent to the primordia; (2) *nucleus* — the area of growth between the central and distal primordia and between the primordia and point of hatch; (3) *freshwater growth* — the region between the point of hatch and the point of saltwater entry for anadromous fish or the last annulus for resident fish (in most samples, these sites were in the summer growth region preceding the first or second annulus); and (4) *saltwater growth* — the summer growth region preceding the last annulus on otoliths of anadromous adults.

All otoliths were sampled in the primordia. Sample sites in other otolith regions were included in initial analyses where we ran a transect of probe sites from the primordia out toward the edge of the otolith. Transects and samples in freshwater growth and saltwater growth regions on the otolith were used only to determine whether patterns in the Sr/Ca ratio were consistent with those anticipated based on anadromy and resulting change in chemistry of the environment. We hypothesized that an elevated Sr/Ca signal should be evident in samples from the primordia of fish of anadromous origin relative to those of resident origin. After Kalish (1990), we expected samples from fish of anadromous origin to show a pattern of elevated Sr in the primordia, reduced Sr in the freshwater growth region, and, if an anadromous adult, elevated Sr in the saltwater growth region.

TABLE 2. Elemental Sr/Ca ratios of 10 sequential microprobe samples of a single site on a single otolith.

Sample in order of analysis	Sr/Ca ratio
1	0.00232
2	0.00176
3	0.00214
4	0.00241
5	0.00202
6	0.00213
7	0.00194
8	0.00237
9	0.00212
10	0.00254

Except for the transects, we sampled six sites within the primordia on each otolith. Analyses of individual sites with high organic content or with surface flaws were eliminated from the data set. Such results were identified by their low total ion concentration (<80% carbonate by weight). Nine otoliths out of the entire sample of 162 were limited to five sites in the primordia.

We analyzed water chemistry to describe the relationship between the chemistry of otolith region and the chemistry of the environment in which the otolith, or yolk precursor in the case of primordia, developed. Water samples were collected from each of the freshwater sources where fish reared except for Takla Lake. Water samples were analyzed by inductively coupled plasma atomic emission spectrometry, according to

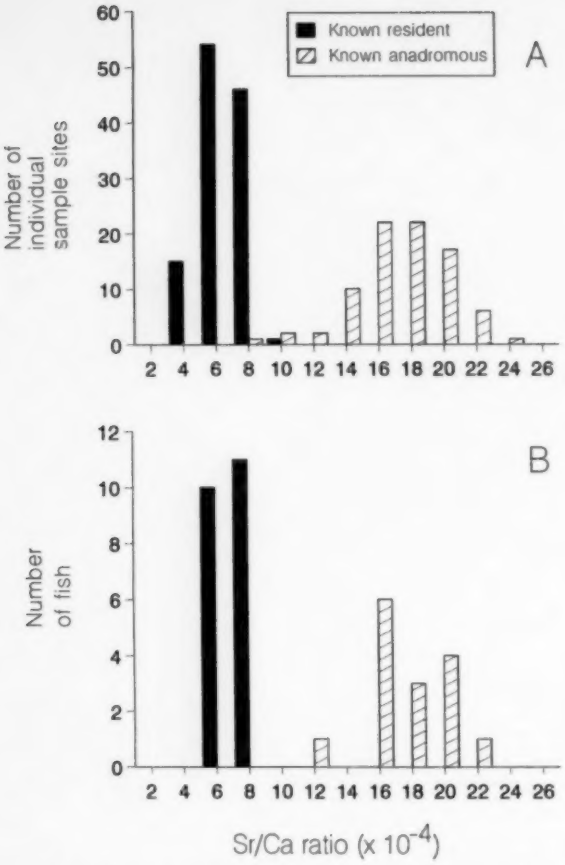

FIG. 2. Frequency distribution of elemental Sr/Ca ratios from microprobe sites in primordia of otoliths from *O. nerka* of known resident or anadromous origin. All fish were the progeny of fish spawned at Redfish Lake. They were incubated at the Eagle Island Hatchery. (A) All sample sites in the primordia for all fish; (B) means of sample sites in the primordia for individual fish. Numbers on the *x*-axis represent the midpoint of bins used in the frequency distributions.

TABLE 3. Concentration (detection limit 0.010 mg·L^{-1}) and elemental ratios of Sr and Ca in three lakes and the Eagle Island Hatchery water supply. Sample sizes are shown in parentheses.

Location	Elemental Ca (mg·L^{-1})	Elemental Sr (mg·L^{-1})	Sr/Ca ratio[a]
Redfish Lake	3.88 (6)	<0.010 (6)	<0.0012
Alturas Lake	8.29 (6)	0.110 (6)	0.0061
Wenatchee Lake	2.00 (1)	0.015 (1)	0.0034
Eagle Island Hatchery	32.00 (2)	0.340 (2)	0.0049

[a]Sr/Ca ratios were calculated as normalized mole fractions.

U.S. Environmental Protection Agency method 215.1 (U.S. Environmental Protection Agency 1983) for Ca, and Standard Methods method 303 (American Public Health Association 1989) for Sr. The detection limit for both elements was considered to be 0.010 mg·L^{-1}. We assumed a Sr/Ca ratio for seawater of 0.00874 (Bruland 1983) for all the otolith sample sites of anadromous origin.

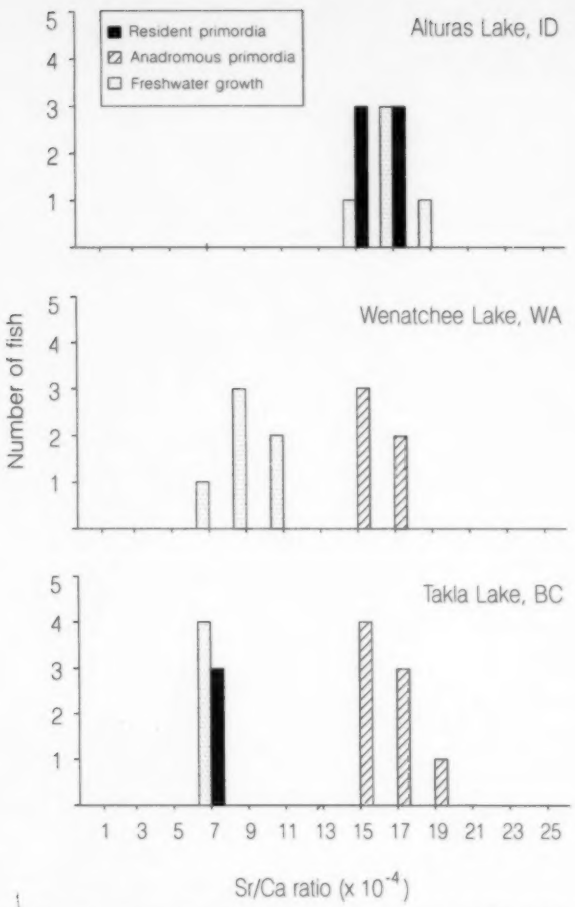

FIG. 3. Frequency distribution of mean elemental Sr/Ca ratios from microprobe sites in primordia and freshwater growth regions on otoliths of individual *O. nerka* from Alturas, Wenatchee, and Takla lakes. The Wenatchee Lake samples are of anadromous origin; the Takla Lake samples are assumed to be of resident, anadromous (but residual), and anadromous origin; the Alturas Lake samples are of resident origin. Numbers on the *x*-axis represent the midpoint of bins used in the frequency distributions.

Results

Samples of Known or Assumed Origin

Microprobe transects across otoliths of known or assumed origin showed patterns consistent with life history. Transects across otoliths from sockeye salmon smolts and adults from Wenatchee Lake showed intermediate Sr/Ca ratios in the primordia and nucleus, lower Sr/Ca ratios in the freshwater growth region, and higher ratios in the saltwater growth region (Fig. 1). Transects run on otoliths from fish of resident origin in Redfish Lake revealed low ratios at all sites (Fig. 1).

The Sr/Ca ratios in the primordia of otoliths of fish of known anadromous origin in Redfish Lake were clearly elevated relative to ratios from otoliths of resident fish

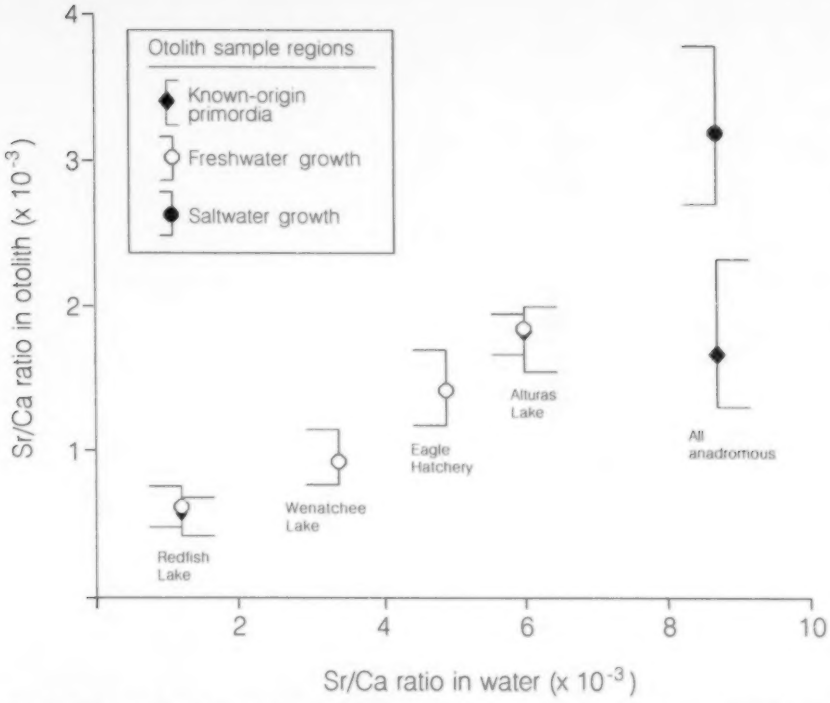

FIG. 4. Relationship of mean elemental Sr/Ca ratios in primordia and freshwater and saltwater growth regions of otoliths and the water chemistry associated with the growth of that area or development of its yolk precursors. Samples are from three lakes and the Eagle Island Hatchery. Samples from all anadromous fish or anadromous origin primordia were pooled from all lakes to relate to the water chemistry for seawater. Vertical bars represent the range of observations.

(Fig. 2A). The distribution of all sample sites in the two groups overlapped, but the distribution of means for individual otoliths did not (Fig. 2B). None of the samples from fish of resident origin produced a mean Sr/Ca ratio higher than 0.00080 (range 0.00042–0.00080), and only one sample from fish of anadromous origin produced a ratio lower than 0.00140 (range 0.00114–0.00201). Student *t*-tests of log $(x + 1)$ transformed ratios between anadromous and resident means for individual otoliths or among all sample sites pooled by origin were significant ($p < 0.001$). The CV among sites within individual otoliths ranged from about 0.04 to 0.20 in both groups.

The sample means of otolith primordia from fish of anadromous origin in Wenatchee and Takla lakes were within the range of the sample means of fish of anadromous origin in Redfish Lake (Fig. 3). Of all 28 anadromous samples (all lakes), only one mean Sr/Ca ratio was below 0.00140. Samples in the primordia of otoliths from resident kokanee in Takla Lake were lower than those in the primordia of anadromous fish and were similar to samples in the primordia of resident fish in Redfish Lake. The samples in primordia of kokanee from Alturas Lake were higher (range 0.00155–0.00204) than those in kokanee from either Redfish or Takla Lake (Fig. 3) and were similar to those observed in samples in the primordia of fish of anadromous origin.

The Sr/Ca ratios in freshwater growth regions on otoliths were similar to those we observed in the primordia of resident fish from the same lake. The mean Sr/Ca ratios in freshwater growth regions were lower than those in the primordia of anadromous origin fish for samples from fish in Redfish, Takla, and Wenatchee lakes. Differences between anadromous primordia and freshwater growth regions were significant ($p < 0.001$) whether for the means of individual otoliths or for all sites in common regions pooled among fish.

Concentrations of Sr and Ca varied substantially among the waters we sampled (Table 3). The resulting Sr/Ca ratios ranged from <0.00120 to 0.00610. We found a direct relationship between the Sr/Ca ratio in primordia, freshwater growth, or saltwater growth regions and the Sr/Ca ratio of the water associated with the development of the otolith sites or their yolk precursors (Fig. 4).

Samples of Unknown Emigrants from Redfish Lake

We completed microprobe analyses on otoliths from 94 individuals that emigrated from Redfish Lake in May 1991. The range of mean Sr/Ca ratios in primordia of individual fish was similar to that observed among pooled samples from fish of resident and anadromous origin (Fig. 5). Two modes were evident in samples from freshwater growth regions. However, all freshwater samples higher than 0.00080 were taken from fish that were held at the Eagle Island Hatchery. The sample sites fell in the region of growth that occurred while the fish were in the hatchery and therefore represent incorporation of Sr that occurred in the hatchery and not in the lake. The range of means from freshwater growth

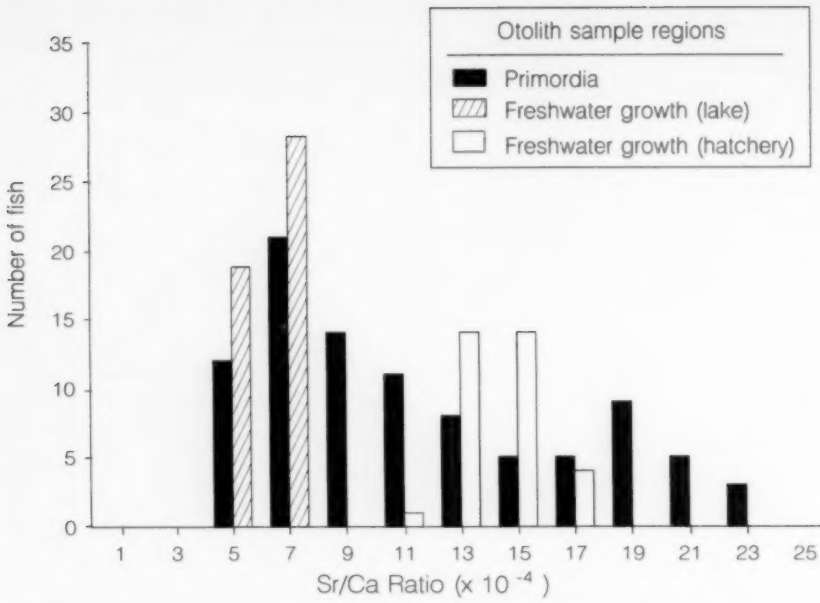

FIG. 5. Frequency distribution of mean elemental Sr/Ca ratios from microprobe sites in primordia and freshwater growth regions on otoliths of individual *O. nerka* trapped while emigrating from Redfish Lake in May 1991 (n = 94). Freshwater sample regions are identified as those that were in areas of growth that occurred in the lake and in the Eagle Island Hatchery. Numbers on the x-axis represent the midpoint of bins used in the frequency distributions.

regions that represented growth in the lake was much narrower and consistent with the range of means from other freshwater samples, except those from Alturas Lake. Two modes were evident in the primordia means, suggesting that the sample included fish of both resident and anadromous origin. We did not find two clearly discrete groups that would allow us to classify the origin of all fish. About one third (35%) of the samples fell into the range between 0.00080 and 0.00140, while 29 and 36% of the samples fell above and below that range, respectively.

The CV among sites within the primordia of individual otoliths ranged from about 0.10 to 0.30. The variation among sample sites in individual otoliths tended to be higher than we observed in the sequential samples at a single site on a single otolith (CV about 0.11) or among sites in the primordia of individuals of known parental origin (0.04–0.20). The variation among sites within the primordia also tended to be higher in samples that fell in the midrange between the two modes (Fig. 6).

The Sr/Ca ratios in primordia of the five anadromous fish that returned to Redfish Lake in 1991 and 1992 fell in the range observed for samples in the primordia of fish of known anadromous origin (Table 4).

Discussion

The patterns we observed in Sr/Ca content of sockeye salmon otoliths were consistent with changes in environment related to life history and with the patterns Kalish (1990) observed for other salmonids. Differences in our known samples of resident and anadromous fish from Redfish Lake were clear, and the expected patterns were evident in other populations as well. The association of otolith and environmental chemistry demonstrates that analysis of Sr content in otoliths of migratory salmonids, including sockeye salmon, can provide information on life history.

There were differences in our results and those of Kalish (1990). The absolute magnitudes of our Sr/Ca ratios in primordia and freshwater growth sites were lower than the observations reported by Kalish (1990) for brown and rainbow trout and Atlantic salmon. Our sample means in otolith primordia of resident fish ranged from about 0.00040 to 0.00080 and in primordia of anadromous fish from about 0.00110 to 0.00230. Kalish (1990) observed ranges in Sr/Ca ratios of about 0.00070–0.00170 and 0.00220–0.00520 for the same two groups, respectively. Our observations in saltwater growth regions, however, were in the same range as those reported by Kalish (1990) (about 0.0025–0.0040, his fig. 1).

A variety of factors including environmental chemistry and stress may influence the mobilization and availability of Ca and Sr in the blood plasma, vitellogenin, the resulting yolk proteins of developing ova, and ultimately in the substitution of Sr for Ca in the matrix of developing otoliths (Kalish 1989). The observed differences of our samples from wild fish relative to the captive (sea farm or hatchery) stocks represented in Kalish's (1990) samples could be explained by differences in life history and environment. The anadromous fish in our samples all moved into freshwater well before spawning (2–4 mo) and undoubtedly experienced a variety of stresses related to the adaptation from salt water to freshwater and the extended migrations (up to 900 km and several months). It is not clear whether yolk development was complete when the sockeye salmon rep-

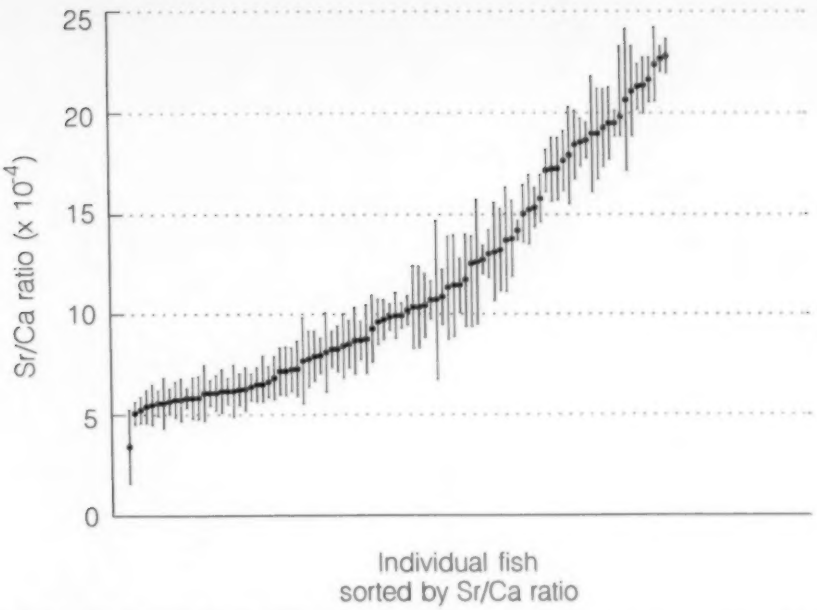

FIG. 6. Mean elemental Sr/Ca ratios from microprobe sites in the primordia of otoliths of individual *O. nerka* trapped while emigrating from Redfish Lake in May 1991. The vertical bars represent ±1 SD.

resented in our samples left the ocean. Regardless, some ion exchange can occur between the female and the egg in the period prior to spawning (Alderdice 1988). Such exchange might continue to influence the yolk content during migration and might explain the lower ratios we observed in primordia of fish of anadromous origin relative to those of Kalish (1990). We observed that the Sr/Ca content in primordia of anadromous fish was typically less than that in saltwater growth regions, while the ratios in primordia of resident fish were similar to those in freshwater growth regions (Fig. 4). The difference suggests some attenuation of the Sr content of the yolk in anadromous females that does not occur in resident females. The anadromous adults in Kalish's (1990) study were held in freshwater for only 3 wk compared with the several months in the migration and staging of sockeye salmon. Substantial differences could result in anadromous primordia through such differences in prespawning environments.

Differences in Sr/Ca ratios among freshwater environments could also explain differences observed in primordia of resident fish between our study and that of Kalish (1990). The variation in freshwater chemistry can clearly influence the Sr content observed in otoliths derived from resident parents. We observed substantial variation in Sr/Ca ratios for the bodies of water represented in our study and a strong association between water chemistry and otolith chemistry. Kalish (1989, 1990) did not report water chemistry for his study sites, but the variation we observed among lakes demonstrates that differences could be large.

Our attempt to characterize the origin of the fish leaving Redfish Lake was equivocal. The samples produced a range and two modes in Sr/Ca ratios indicating that migrants of both resident and anadromous origin were present. The sample distributions, however, did not break into two clearly discrete groups. None of our known Redfish primordia samples had mean Sr/Ca ratios above 0.00080 or below 0.00110. Only 1 of the 28 known anadromous samples from all lakes fell below 0.00140. About one third of the 94 unknown samples were between 0.00080 and 0.00140.

TABLE 4. Mean elemental Sr/Ca ratios from microprobe sites in the primordia of otoliths of five anadromous *O. nerka* that returned to Redfish Lake in 1991 and 1992.

1991	
Female	0.00233
Male A	0.00213
Male B	0.00175
Male C	0.00131
1992	
Male	0.00223

There are two possible reasons for the lack of resolution. First, the increased variability in the known samples could have been due to analytical error. The variability among samples sites within an otolith tended to be higher in the samples that were in the range of intermediate Sr/Ca ratios. As a precaution, we reexamined the otolith preparations and sample sites for each sample that fell in the intermediate range. We found no evidence of poor sample preparation, site selection outside a primordia, or surface flaws that could have contributed to any unusual variation.

Second, our sample size of fish of known origin may not have described the full variability inherent in otolith chemistry of the wild resident fish. Our known sample included only fish from the Fishhook Creek kokanee stock. It is possible that another group of fish may have contributed to the

emigration. We recently observed a small group of resident or residual fish spawning along the lake shore. Our known samples were incubated in a relatively stable hatchery environment. Each individual experienced essentially identical conditions of water temperature and chemistry. Embryos from wild fish incubate in a range of conditions that are found in both Fishhook Creek and along the lake shore. Eggs may be ionically permeable and exhibit active uptake of Ca (and presumably Sr) at fertilization (Alderdice 1988; S. Schroder, Washington Department of Fisheries, Olympia, Wash., personal communication). Differences in the chemistry of the incubation microhabitats caused by groundwater or local tributary influences could contribute to additional variability in otolith chemistry (J. Kalish, Ministry of Agriculture and Fisheries, Wellington, N.Z., personal communication). Some studies have also suggested that the Sr/Ca ratio in otoliths can be related to temperature (Radtke et al. 1990; review in Toole and Nielsen 1992) or rate of growth (Kalish 1989; Sadovy and Severin 1992). Temperature during incubation can influence the growth and number of otolith primordia that develop in other salmonids (Neilson et al. 1985) and might well influence the physiology of Ca deposition. Temperatures among and within the spawning habitats in Redfish Lake may vary by 10°C and could well have influenced variation in otolith chemistry.

Our results indicate that the utility of otolith microchemistry will be highly dependent on the variation in chemistry of freshwaters and on variation in timing and length of exposure to those waters. The observed variation in chemistry among lakes, for example, could seriously confound attempts to discriminate resident and anadromous fish. The Sr/Ca ratios we observed in Alturas Lake kokanee otoliths were similar to ratios observed in primordia from fish of anadromous origin in other lakes. If anadromous fish were present in Alturas Lake, it would be impossible to distinguish their progeny from those of resident fish. Clearly, the simple assumption that freshwater Sr/Ca ratios are less than those in seawater is inappropriate. Detailed water chemistry should be part of any further application.

Experimentation with spawning and incubation environments might explain the lack of resolution in our unknown samples from Redfish Lake. Collection of known-origin samples in the wild might also be possible by trapping emergent fry following observation of known-female spawning. Until that work can be done, however, further studies attempting to discriminate the origin of fish in Redfish Lake or any other system will be vulnerable to the same uncertainties.

We cannot conclude that resident fish are successfully producing anadromous adults in Redfish Lake. The chemistries of all five anadromous adults that returned to Redfish Lake in 1991 were consistent with an anadromous origin. Our data did indicate that both resident and anadromous fish were present among the 1991 emigrants and that resident fish represented a large if not dominant proportion of the sample. The potential for anadromous behavior has apparently been retained in fish from resident parents but we cannot, as yet, estimate the rate of emigration or its contribution to anadromous returns.

Acknowledgments

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Temporal Variation in Size and Abundance of Juvenile Atlantic Cod (*Gadus morhua*) at an Inshore Site off Eastern Newfoundland

David A. Methven and Christopher Bajdik

Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, NF A1C 5S7, Canada

Methven, D.A., and C. Bajdik. 1994. Temporal variation in size and abundance of juvenile Atlantic cod (*Gadus morhua*) at an inshore site off eastern Newfoundland. Can. J. Fish. Aquat. Sci. 51: 78–90.

Temporal variability in abundance and size of juvenile Atlantic cod (*Gadus morhua*) was studied at a shallow-water site in Trinity Bay, Newfoundland, from July 1982 to September 1983 and July 1989 to September 1990. Cod were collected with a small seine during the day and night. 0-group and 1-group cod predominated in the catch. Nighttime catches contained significantly more and larger cod than daytime catches primarily because 1-group cod were only collected at night. 1-group cod were not collected when water temperatures were less than 0°C or when ice was present. Abundance peaked in August–November and April–June. Pelagic juveniles arrived inshore when water temperatures and salinities were highest (>12°C, >30 ppt) in August and September and represented ~25–40 and 10%, respectively, of the cod collected at that time. Significantly more cod were collected in 1989–90 than in 1982–83, although water temperatures were not significantly different between the two periods. Sampling by additional fishing gears, including SCUBA observations, supports the hypothesis that 0-group and 1-group cod move into the sampling area at night (or dusk) and that daytime gear avoidance is secondary to diel activity patterns in explaining differences in day and night catches.

La variabilité temporelle de l'abondance et de la taille de la morue franche juvénile (*Gadus morhua*) a été étudiée dans un endroit de la baie Trinité (Terre-Neuve) où l'eau est peu profonde, de juillet 1982 à septembre 1983 et de juillet 1989 à septembre 1990. Le prélèvement des morues a été effectué au moyen d'une senne de petite taille, le jour et la nuit. Les morues du groupe 0 et du groupe 1 étaient prédominantes dans les prises. Les prises effectuées la nuit contenaient beaucoup plus de morues et de plus grande taille que les prises effectuées le jour, surtout parce que les morues du groupe 1 n'étaient prélevées que pendant la nuit. On ne capturait pas les morues du groupe 1 lorsque la température de l'eau était inférieure à 0 °C ou en présence de glace. L'abondance a atteint un pic entre août et novembre et entre avril et juin. Les juvéniles pélagiques sont arrivés dans les eaux côtières lorsque la température et la salinité étaient les plus élevées (> 12 °C, > 30 ppt) en août et en septembre et représentaient, respectivement, environ 25 à 40 et 10 % des morues prélevées à ce moment-là. Un nombre beaucoup plus important de morues ont été prélevées en 1989–1990 qu'en 1982–1983, même si la température de l'eau n'était pas significativement différente entre les deux périodes. L'échantillonnage au moyen d'autres engins de pêche, notamment des observations en plongée autonome, soutient l'hypothèse selon laquelle les morues de groupe 0 et de groupe 1 migrent dans l'aire d'échantillonnage la nuit (ou à la tombée du jour) et que l'évitement des engins pendant le jour est secondaire aux profils d'activités nycthémérales pour expliquer les différences entre les prises pendant le jour et pendant la nuit.

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Harden Jones's (1968) concept of a circuit of migration between spawning grounds, summer feeding areas, and nursery areas appears to be applicable to many gadids, including Atlantic cod (*Gadus morhua*) in the Newfoundland region. Exceptions to this generalization are numerous, however, and include inshore spawning (Thompson 1943; Templeman 1964, 1979), large cod remaining in coastal regions year-round, and 0-group cod settling offshore (Serebryakov 1968). However, most cod in the Newfoundland region traditionally spawn on the Labrador and northeast Newfoundland shelves at depths >250 m in March–April (Lear and Green 1984). An inshore movement occurs in May–June when cod feed heavily on capelin (*Mallotus villosus*) prior to moving offshore again in late summer and fall (Templeman 1965; Pinhorn 1984; Lilly 1987; Methven and Piatt 1989). Eggs and larvae develop as they drift southward with the Labrador Current, with 0-group juveniles occurring in both nearshore and offshore areas in autumn (Serebryakov 1968; Lear et al. 1980; Lear and Green 1984; Lear and Wells 1984).

The importance of nearshore nursery areas for juvenile fishes is well documented (Haedrich 1983), especially in European waters (Daan 1978; Rauck and Zijlstra 1978; Godø et al. 1989), where juvenile cod have been monitored for many years to obtain estimates of year class strength (Tveite 1984; Johannessen and Tveite 1989). Large concentrations of juvenile cod in coastal regions of eastern Newfoundland have also been reported (Fleming 1963; Lear et al. 1980), although the abundance of juvenile cod has not been consistently reflected in estimates of (adult) stock size (Lear et al. 1980). Explanations proposed for inconsistencies between the abundance of juveniles and adult stock size include a lack of standardization of fishing gear and variability in abiotic factors including wind, tide, temperature,

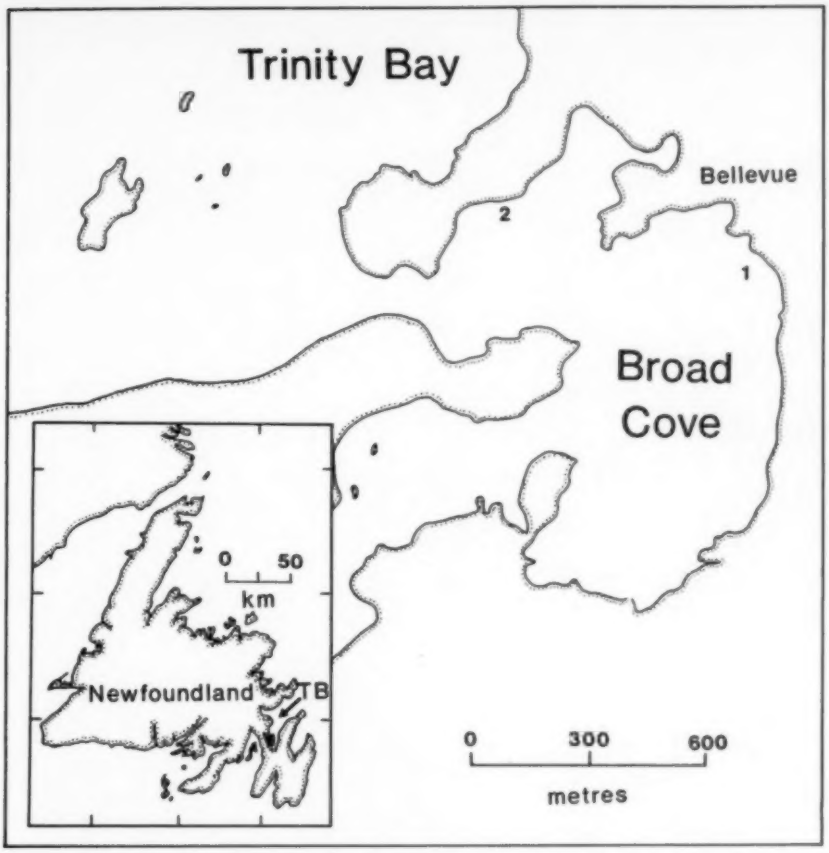

FIG. 1. Map of Newfoundland showing the primary (1) and secondary (2) collection sites at Bellevue, Newfoundland. TB = Trinity Bay.

and waves during sampling (Lear et al. 1980). Furthermore, although the importance of nearshore nursery areas for juvenile fishes is well known, their significance to overall recruitment remains generally unknown (Olsen and Soldal 1989; Koutsikopoulos et al. 1991).

There are many unanswered questions regarding the population dynamics of juvenile and adult cod in the Newfoundland region despite their economic importance to local and international economies for hundreds of years. One such question concerns the extent of temporal variation in size and abundance of juvenile cod that occur inshore along the coast of Newfoundland (Lear et al. 1980; Lear and Green 1984). Our objectives in this study were to address this question by determining the variation in size and abundance of juveniles at a single inshore sampling site over diel, seasonal, and annual time scales. Fishing effort was standardized throughout the study and variation due to substrate type and depth remained constant. Statistical tests were performed on two sets of hypotheses: (1) hypotheses concerning differences between daytime and nighttime collections and (2) hypotheses concerning differences between two 16-mo series of collections made 6 yr apart. We tested the null hypothesis of no differences in size and catch of cod between both day and night collections and the two 16-mo series of collections.

Materials and Methods

Study Site

Collections of juvenile cod were made at Bellevue, Trinity Bay, Newfoundland (Fig. 1; 47°38′N, 53°43′W). These collections extend the observations of Brown et al. (1989) for 0-group cod at the same site. The site was chosen because the bottom was relatively flat and free of obstructions and because salinity was usually high (>25 ppt).

The primary sampling site (1, Fig. 1) is relatively protected. The bottom consists primarily of small rocks and gravel. The difference between high and low tide is about 1.2 m and the gently sloping flat bottom ensures a relatively large intertidal zone of 20 m horizontal distance at low tide suitable for towing the small seine. A comparable secondary site (2, Fig. 1) was sampled on four occasions during winter 1983 when the primary site was blocked by ice. The main hydrographic feature of the area is a shallow inlet that connects Broad Cove to Trinity Bay. Tidal currents through this inlet average 0.21 m/s at midtide (range = 0.05–0.94 m/s). Additional details on the study site are in Gilkinson and Methven (1991).

Sampling Cod with a Small Seine

Cod were collected with a small nearshore seine (9 m

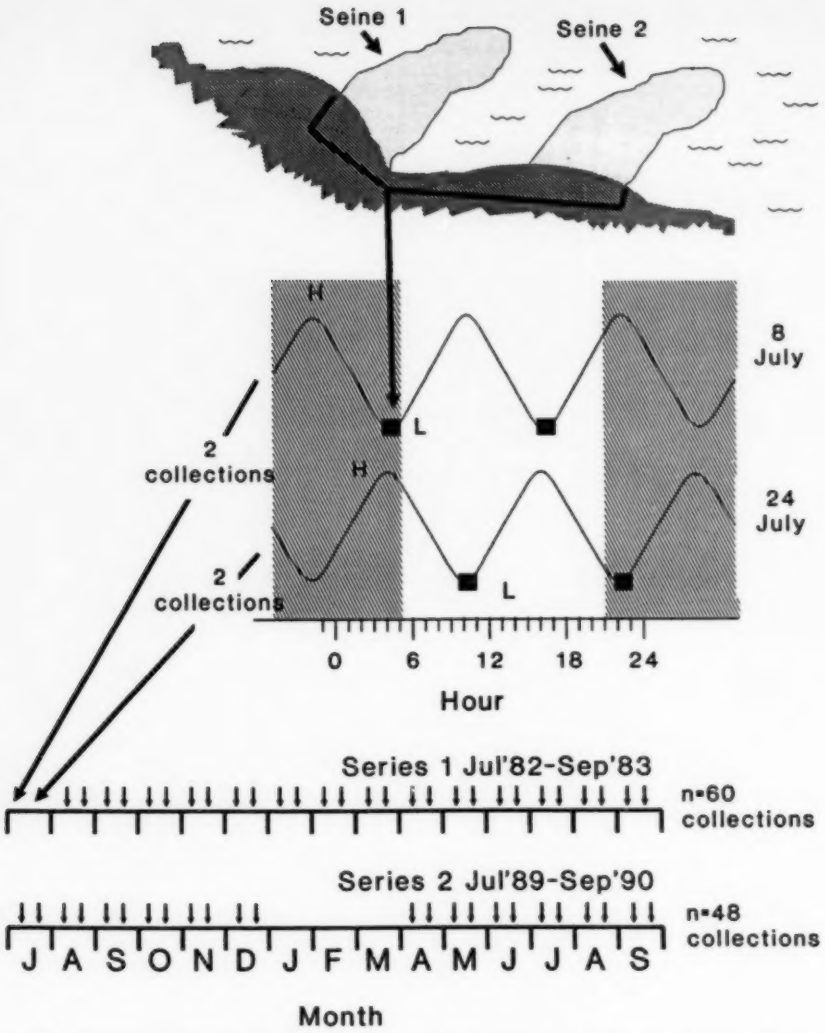

FIG. 2. Summary of the sampling design based on paired comparisons of day and night collections of cod. The cod collected from two seine hauls (Seine 1 and Seine 2) were combined to produce one collection (darkened box) of fish. Two collections were made during the first half (e.g., 8 July) and the second half (e.g., 24 July) of each month, always at low (L) tide. Nighttime is indicated by the shaded areas. Refer to text for additional details.

long × 1.5 m deep; 9-mm stretched mesh throughout) equipped with a large collection bag. Small floats located on the headrope and small lead weights attached to the footrope were spaced at 55- and 25-cm intervals, respectively. Two wooden poles, each about 2 m long, were tied to the headrope and footrope at each end of the seine. The seine was pulled through the water (maximum depth 1.2 m) by two people wearing chest waders. That portion of the seine attached to the wooden poles by the footrope was always in contact with the bottom to keep escapement to a minimum. The seine fished throughout the water column from the surface to the bottom.

Four collections of fish were made each month (Fig. 2). Two pairs of collections were taken, one pair during the first half and one pair during the second half of each month, such that the pairs of collections were usually about 2 wk apart. Each collection consisted of two seine hauls that started and finished at the same locations on the shore, thereby keeping the area sampled constant for each collection. Samplings within each pair of collections were about 12–13 h apart such that only consecutive low tides were sampled, one usually during the day and one usually at night. Sampling was conducted from July 1982 to September 1983 (Series 1) and from July 1989 to September 1990 (Series 2). It was not possible to deploy the seine in January, February, and March 1990 because of the presence of landfast ice. All fish from each collection (i.e., two seine hauls) were combined and preserved in 5% formalin.

Surface (upper 5 cm) water temperatures were measured and water samples were taken from the surface (1982–83) and

bottom (0.9–1.2 m; 1989–90) for salinity determination (Autosal model 1800 salinometer, Guideline Instruments) immediately after each collection of fish. Temperature and salinity were measured to determine if these were important in influencing diel, seasonal, and/or annual catches of cod.

Cod were sorted, measured for standard length (SL) to the nearest 0.1 mm with dial callipers, and weighed to the nearest 0.1 g. Cod were assigned an age (0-group or 1-group) based on changes in length frequency modes. 0-group cod refers to the 1982 (Series 1) and 1989 (Series 2) year classes. 1-group cod refers to the 1981 (Series 1) and 1988 (Series 2) year classes. It is possible that some large juveniles classified as age-1 were actually age-2 fish and belonged to the 1980 and 1987 year classes.

Additional Sampling

Additional sampling at the primary site was conducted to determine the diel pattern in abundance and to observe if juvenile cod were avoiding the small 9-m seine. Five different types of sampling gear/methods were used: small (described above) and large seines, gill nets, bottom trawl, and SCUBA observations. Depth of sampling depended on the fishing gear but was usually less than 4 m.

A total of 48 seine hauls (24 collections) were conducted over 24 h on 21–22 August 1982. Fishing effort was constant, with two seine hauls being conducted each hour with the 9 × 1.5 m seine. The maximum depth of water sampled was ~1.2 m. In addition, a much larger seine (27.4 × 1.8 m; 22-mm stretched mesh) with a collection bag was deployed three times during the day at low tide and three times at night at low tide on 13–14 October 1990.

A large gill net (60.9 × 2 m; 30-mm stretched mesh) was quickly deployed from a 4.5-m inflatable boat on 24–25 September 1983. The gill net was deployed once during the day and once at night at low tide. The net was set in a semicircle starting and ending at the shore and was hauled in slowly towards shore.

Three small gill nets spaced ~60 m apart were set perpendicular to shore during the day (depth = 2.5 m) and night (depth = 2.2 m) on 16–17 October 1991. Each gill net was 22.9 m long × 2.4 m deep and contained three different mesh sizes (25-, 38-, and 51-mm stretched mesh). Catch per unit effort was calculated by dividing the number of cod collected by the number of hours the nets soaked.

Twenty-four SCUBA dives were conducted along a fixed underwater transect on 24–25 September 1983. The transect extended offshore for ~75 m, ran parallel to the shore for 25 m, and extended 75 m back to shore. One 25-min dive was conducted each hour. The maximum depth surveyed was 4 m. Types of bottom habitat observed included small rocks and gravel and mud–silt. No bedrock or kelp–*Fucus* habitat was seen. All cod observed within 3 m of either side of the transect were counted. It was not possible to positively identify all cod as *G. morhua* when diving because Atlantic cod can be confused with the morphometrically similar Greenland or rock cod (*Gadus ogac*). Greenland cod also occur inshore at Bellevue and along the northeast coast of Newfoundland. Divers used underwater lights at night and recorded information on plastic slates. Length, weight, and age information were not collected.

A 4.9-m semiballoon bottom trawl (5.1-m headrope and 6.4-m footrope) made of nylon netting (38-mm stretched mesh throughout, with a 9-mm stretched mesh liner in the codend) was towed at the site throughout autumn 1991. All tows were conducted in water <4.0 m deep. Twelve paired day and night collections were made. Most tows were conducted just after sunset (night) and just after sunrise (day). The duration of most tows was 10 min.

Data Analysis

Statistical tests were performed for two sets of hypotheses: (1) those concerning differences between daytime and nighttime collections (1982–83 and 1989–90 data analyzed separately) and (2) those concerning differences between the 1982–83 collections and the 1989–90 collections. Between-series analyses were conducted only on nighttime collections because the vast majority of cod were collected at night. Analyses were initially conducted without separating the age classes. Age classes (0-group and 1-group) were separated in subsequent analyses. The level of significance for all statistical tests was $p < 0.05$; p values >0.10 are reported as $p > 0.10$. All analyses were performed using SAS statistical software (SAS 1988).

Analyses of water temperature, salinity, and number of fish caught were conducted on the difference between the daytime and nighttime values within each pair of observations (i.e., the nighttime value minus the daytime value) for 1982–83 and 1989–90 separately. For cases where both values were recorded during the day, or where both were recorded at night, that pair was excluded from the analysis. There were 27 pairs of observations included in the 1982–83 analysis and 18 pairs included in the 1989–90 analysis. All the differenced variables were tested for normality. Only the temperature differences in 1989–90 were normally distributed. The nonparametric signed rank statistic (SRS) was used to test all night-versus-day hypotheses.

Analyses were also performed to test for differences in temperature, salinity, and the number of fish in 1982–83 versus 1989–90 nighttime collections. Data from the two series were paired by date of capture (to within a week) producing 20 pairs of observations, and differences between the paired values (1982–83 minus 1989–90) were calculated. The differenced values for temperature and salinity were normally distributed and analyzed by simple ANOVA with the pair defining a blocking variable. Differenced values for number of fish caught were not normally distributed, and therefore, the SRS was used.

Results

Temperature and Salinity

Nighttime temperatures averaged 1.1°C colder than daytime temperatures in 1982–83 and 0.4°C colder in 1989–90. Night–day differences in temperature were significant in 1982–83 (SRS = -84, $p = 0.0002$) but not in 1989–90 (SRS = −38, $p > 0.10$). Temperature was highest (16–18°C) in July–September and lowest in December–February (<0°C, usually when ice was present). Autumn (September–November) and spring (April–May) were periods of rapid temperature change, there being approximately 10°C decrease in temperature in autumn (~14–4°C) and a 7°C increase in spring (~3–10°C). There was no significant difference in temperatures between 1982–83 and 1989–90 (ANOVA, $F = 2.00$, df = 1,19, $p = 0.1735$).

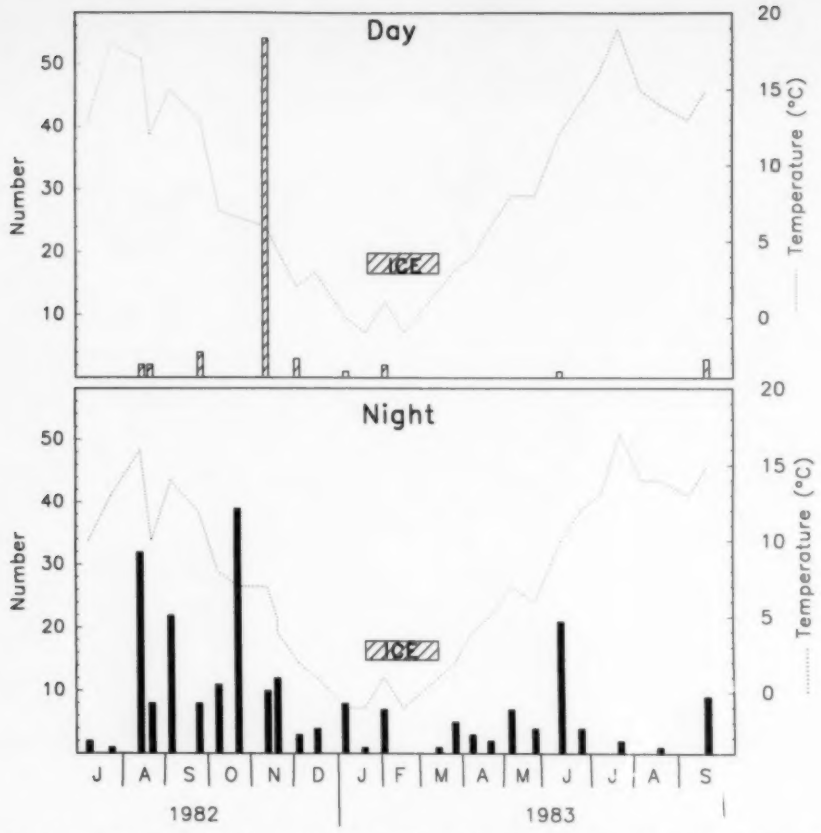

FIG. 3. Number of fish in day and night catches of 0-group and 1-group cod in relation to time of year, water temperature, and ice in 1982–83. Fishing effort was equal for each collection.

TABLE 1. Total number, mean length (mm SL), and mean weight (g) of all cod caught (SE in parentheses).

		1982–83		1989–90	
Age		Day	Night	Day	Night
0+	Total *n*	69	224	53	753
	Mean length	64.4 (1.6)	69.7 (1.7)	45.3 (2.1)	85.0 (1.1)
	Mean weight	3.2 (0.3)	4.4 (0.4)[a]	1.2 (0.2)	9.0 (0.4)
1+	Total *n*	0	26	0	67
	Mean length	—	162.8 (6.1)	—	175.0 (4.2)
	Mean weight	—	55.7 (6.7)	—	67.8 (5.1)

[a]*n* = 215.

There was no significant difference in salinity between day and night within either series of collections (1982–83: SRS = 22.5, $p > 0.10$; 1989–90: SRS = 7.5, $p > 0.10$). Salinity ranged from 18 to 31 ppt in 1982–83 (mean = 26.3, SD = 2.9, $n = 60$) and from 23 to 32 ppt in 1989–90 (mean = 28.6, SD = 3.1, $n = 46$). There was a significant difference in salinity between 1982–83 and 1989–90 (ANOVA, $F = 6.91$, df = 1,19, $p = 0.0165$), most likely due to sampling at the surface (<5 cm) in 1982–83 and at the bottom (0.9–1.2 m) in 1989–90.

Fish

Three hundred and nineteen cod were caught from July 1982 to September 1983 (Table 1). Two hundred and fifty were collected at night (78.3%) and 69 were taken during the day (21.6%). Night and day catches differed significantly (SRS = 104.5, $p = 0.0001$), there being 3.6 cod collected at night for each cod taken during the day (Fig. 3). Twenty-six of 33 (78.7%) night and 9 of 27 (33.3%) day collections captured cod in 1982–83 (Table 2). Average catch

TABLE 2. Number of collections and mean number of cod caught per collection (SE in parentheses).

		1982–83		1989–90	
	Age	Day	Night	Day	Night
Number of collections		27	33	26	22
	0+	2.6 (2.0)	6.8 (1.6)	2.0 (1.1)	34.2 (7.0)
	1+	0.0 (0.0)	0.8 (0.2)	0.0 (0.0)	3.0 (0.9)

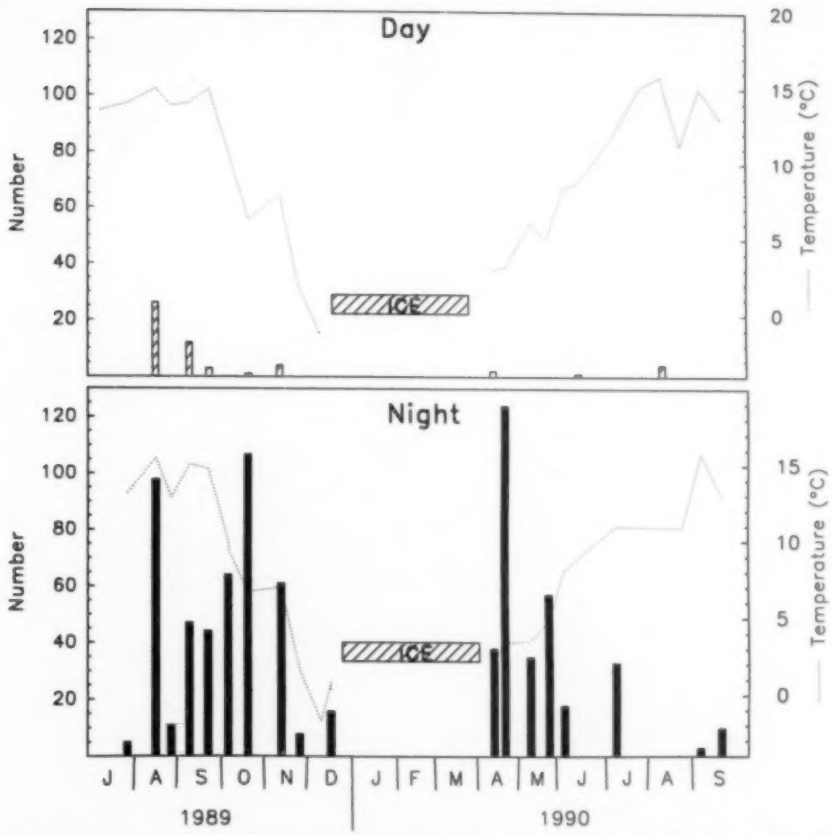

FIG. 4. Number of fish in day and night catches of 0-group and 1-group cod in relation to time of year, water temperature, and ice in 1989–90. Fishing effort was equal for each collection.

rates were greater at night for both 0-group and 1-group cod (Table 2).

Eight hundred seventy-three cod were collected during 1989–90, with 820 (93.9%) caught at night for a night to day ratio of 15.5:1 (Table 1). Catch rates of cod differed significantly between night and day (SRS = 68.0, $p = 0.0001$) (Fig. 4). Eighteen of 22 (81.8%) night and 8 of 26 (30.7%) day seinings collected 0-group cod in 1989–90, for average day and night catch rates of 2.0 and 34.2, respectively (Table 2). Analysis of night and day catches by age class indicated that significantly more 0-group and 1-group cod were caught at night in 1982–83 and 1989–90 (SRS > 27.5 in all cases, $p < 0.002$ in all cases). 1-group cod were only collected at night (Tables 1 and 2).

Catches peaked in August–November 1982 and June 1983 (Fig. 3) and in August–November 1989 and April–May 1990 (Fig. 4). Initial peaks in abundance in August (1982 and 1989) were due primarily to newly arrived pelagic juveniles, which accounted for ~25–40% of the cod collected in August and ~10% in September. 0-group cod accounted for 91.6% (Series 1) and 92.3% (Series 2) of all cod collected. Pelagic juveniles were distinguished from their demersal counterparts by their smaller size (<45–50 mm SL), pelagic coloration (usually evident on individuals <30 mm SL), and the absence of the encysted metacercaria of the digenean *Cryptocotyle lingua* often evident on larger (>55 mm SL), more demersal cod inhabiting the very nearshore zone. Significantly more cod (0-group: SRS = −62, $p = 0.0018$;

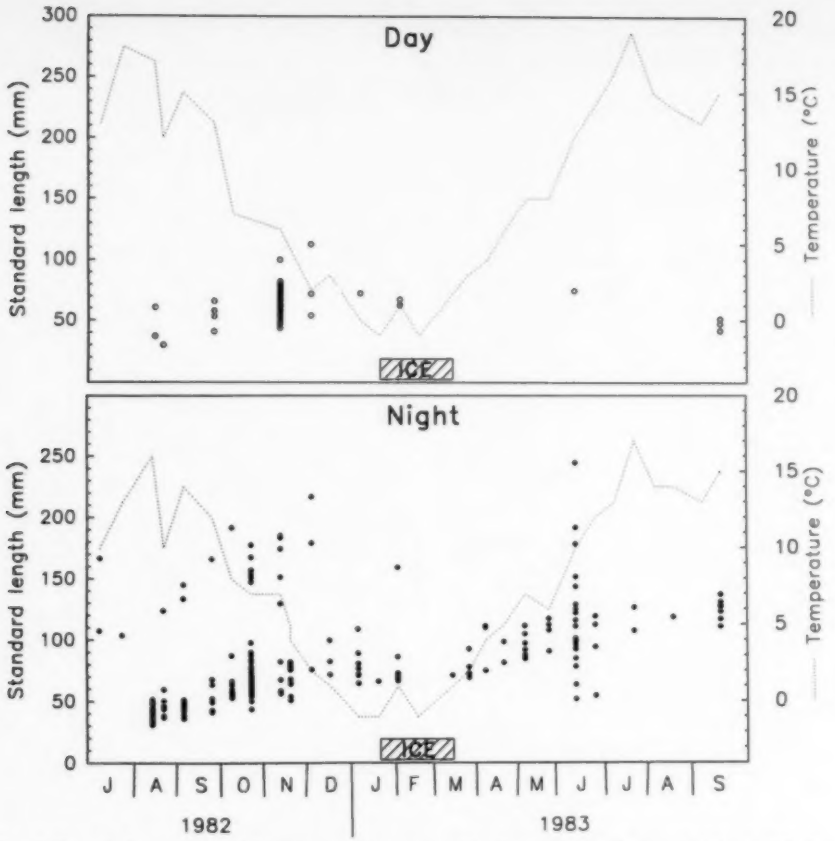

FIG. 5. Length frequencies of 0-group and 1-group cod in day (open circles) and night (solid circles) collections in relation to time of year, water temperature, and ice in 1982–83.

1-group: SRS = −30, $p = 0.0151$) were collected in 1989–90 (Table 2).

Cod caught at night were significantly larger (1982–83: ANOVA, $F = 19.89$, df = 1,157, $p = 0.0001$; 1989–90: ANOVA, $F = 24.04$, df = 1,436, $p = 0.0001$) than those caught during the day (Table 1). This difference was due, in part, to the occurrence of larger 1-group cod that were collected only at night (Fig. 5 and 6). 0-group cod caught at night were significantly larger than those caught during the day in 1989–90 (ANOVA, $F = 33.38$, df = 1,671, $p < 0.0001$) but no differences in length of 0-group cod were observed between night and day collections in 1982–83 (ANOVA, $F = 1.30$, df = 1,202, $p > 0.10$).

Cod were caught at temperatures ranging from −1.7 to 17°C (Fig. 7). Most demersal 0-group and 1-group cod were caught at 4–10°C in 1982–83 and 2–11°C in 1989–90. Pelagic 0-group cod were generally caught at temperatures of 12–16°C in 1982–83 and 13–16°C in 1989–90 (Fig. 7). 1-group cod were collected within a narrower temperature range (1–16°C) than 0-group cod (−1.7–17°C) and not at temperatures <0°C (Fig. 7).

Demersal 0-group cod were collected at 22–30 ppt in 1982–83 and at 23–32 ppt in 1989–90 (Fig. 8). Pelagic juveniles were collected in high-salinity (30–31 ppt) water in 1989–90. Comparisons cannot be made with 1982–83 because salinity measurements were made on surface water samples.

Additional Sampling

One hundred and fifteen cod were collected by the 9 × 1.5 m seine during a 24-h period on 21–22 August 1982 (Fig. 9). Cod collected at night were larger (mean = 52.4 mm SL, SE = 2.6) and more abundant ($n = 107$) than those collected during the day (mean = 30.1 mm SL, SE = 1.5, $n = 8$). The 22.3-mm SL difference in mean lengths was due to the presence of larger 1-group cod that were collected only at night.

Only one 0-group cod (68.0 mm SL) was collected with the large 27.4-m seine (22-m stretched mesh) deployed during the day on 13–14 October 1990. More 0-group cod might have been caught during both day and night if the mesh size had been smaller. Fifty 1-group (mean SL = 172.9 mm, SE = 3.9) and three 0-group (mean SL = 83.3 mm, SE = 5.4) cod were collected by this gear at night.

Twenty-three cod were observed by SCUBA divers on 24–25 September 1983: 10 (43.4%) at night, five at dawn, five at dusk, and three during the day. No cod were caught with the large gill nets hauled during that day. Twelve 1-group cod (164.3 mm SL, SE = 4.4) were collected by the same gear at night. The 30-mm stretched mesh did not retain 0-group cod very well.

The three smaller gill nets set during the day on 16–17 October 1991 caught three juvenile cod (mean = 231.6 mm SL, SE = 39.2) compared with the nighttime

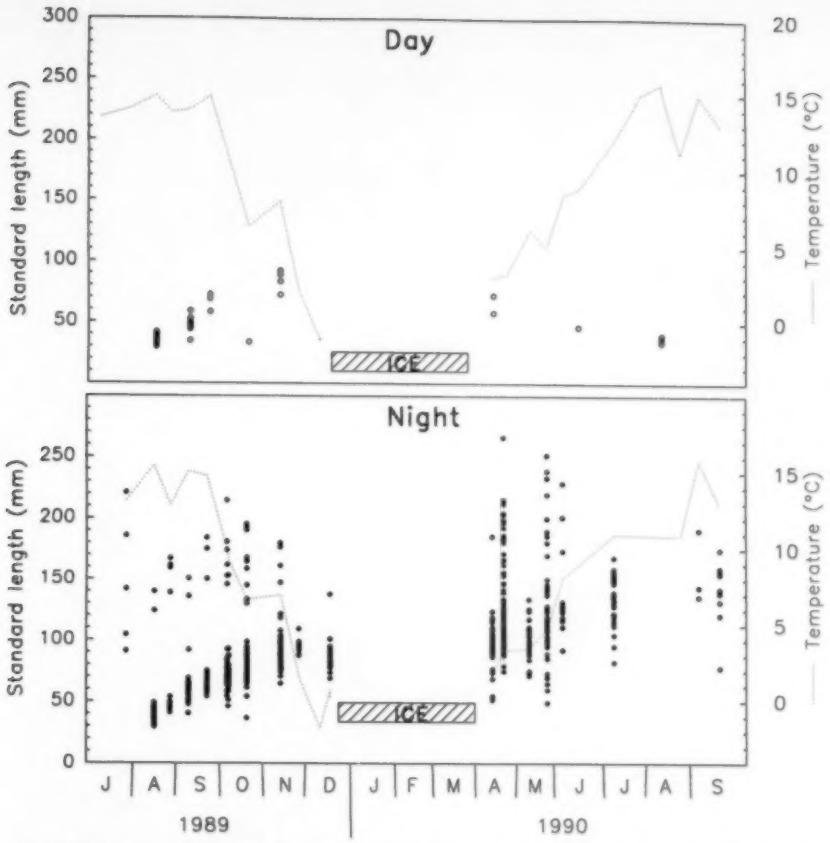

FIG. 6. Length frequencies of 0-group and 1-group cod in day (open circles) and night (solid circles) collections in relation to time of year, water temperature, and ice in 1989–90.

catch of 12 cod (mean = 222.1 mm SL, SE = 19.4). This is a catch rate of 0.23 cod/h during the day and 0.85 cod/h at night.

The 12 paired day–night trawls conducted throughout autumn 1991 collected 42 and 66 juvenile cod during the day and night, respectively. Cod collected at night averaged 117 mm SL (SE = 4.16) whereas cod taken during the day averaged 97 mm SL (SE = 5.72).

Discussion

Repeated sampling of juvenile cod with a small seine in shallow water indicated that abundance and size of cod varied between day and night, seasonally, and from year to year. Significantly more and larger cod were collected at night. The lower catches of 0-group cod and the absence of 1-group cod during the day suggest that small juvenile cod do not occur in shallow (<1.2 m) water in significant numbers during the day and that movement into the sampling site takes place at night or at dusk.

An alternate hypothesis is that gear avoidance occurs during the day. We examined the two possibilities by utilizing several additional fishing gears and methods. Results from all the sampling (which included active and passive fishing gears in addition to SCUBA diving) consistently indicated that, as with the small seine, highest catches were taken at night. The evidence, therefore, suggests that 0-group and especially 1-group cod move into the sampling area at night. These findings suggest that if gear avoidance is occurring, it is secondary to diel activity patterns in explaining the differences between day and night catches. Our findings support the hypothesis that juvenile (1-group and 2-group) cod spend the day in deeper water (Keats 1990). They are also in agreement with the observations of cod made by Clark and Green (1990), who concluded that large (28.6–33 cm) sonic tagged cod were nocturnal and moved between deep, cool-water resting sites (daytime) and shallow, warmer feeding areas (nighttime) during summer.

Variation in the number and size of cod in this study is also due to seasonal differences. Juvenile cod were abundant from mid-August to November and from April to June. Although some cod (primarily those <120–130 mm SL) were collected throughout the year, abundance was reduced in winter and summer. Pihl (1982) reported similar peaks in abundance for 1-group cod in September–October and April–June in a shallow (~1 m) embayment off the west coast of Sweden. Cod migrated into the bay, presumably from deeper overwintering sites, in March–April, after ice break-up. Macdonald et al. (1984) reported similar movements of juvenile cod from a shallow summer habitat to a deeper winter habitat in Passamaquoddy Bay, Bay of Fundy.

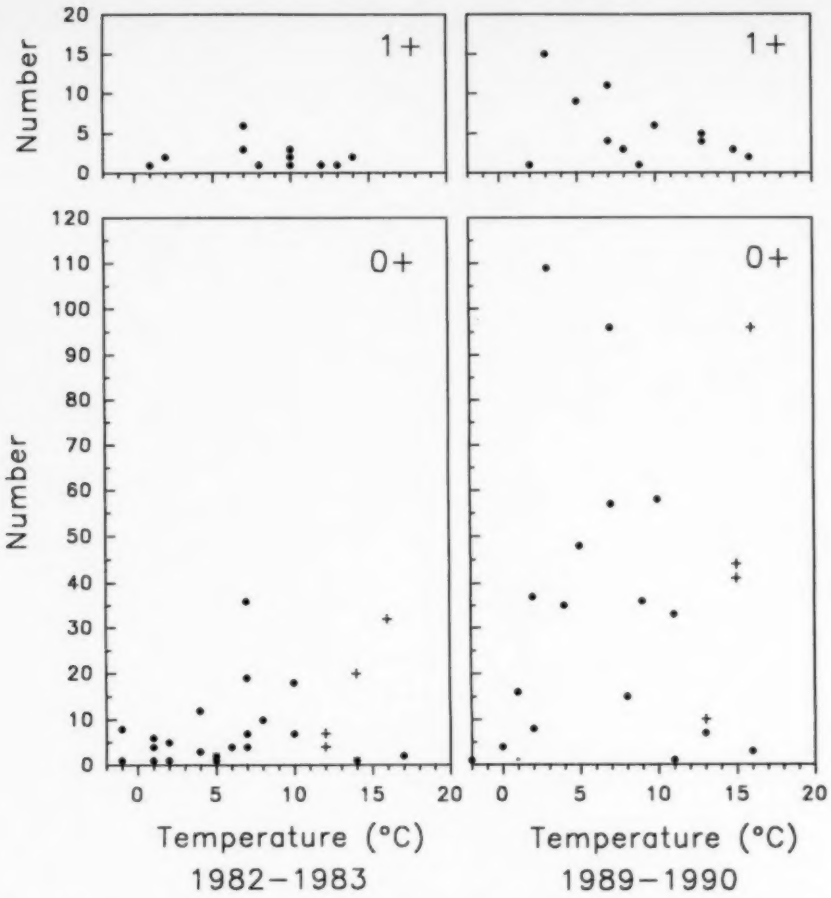

FIG. 7. Number of 0-group and 1-group cod caught in relation to temperature. Crosses = collections containing pelagic juvenile cod. Only data from nighttime catches are presented.

The overwintering sites for juvenile cod in the Newfoundland region are generally unknown. Figures 3 and 4 of this study show lower catches in late November and December. This suggests a time of increased mortality and or movement away from the shallow (<1.2 m) coastal region, presumably to deeper overwintering sites. If juvenile cod do migrate offshore to deeper water (Macdonald et al. 1984) in November–January, then (i) 1-group cod move offshore before 0-group cod as indicated by an earlier decrease in catches in November–December 1982 and 1989 relative to 0-group cod and (ii) some juvenile cod (primarily 0-group) remain in shallow (<1.2 m) subzero water throughout winter even when ice is present (1982–83). Laboratory trials on 0-group, 1-group, and 2-group cod suggest that these fish are physiologically prepared to survive in icy subzero water due to elevated antifreeze levels in the blood (Goddard et al. 1992). Catches of juvenile cod declined in late November–early December and increased again in March–April when water temperatures were ~2–3°C, the induction temperature for antifreeze production in 1-group cod. If the lower catch of cod is due to an offshore movement in November–December, then water temperatures of 2–3°C may signal the beginning of both the movement offshore as well as the movement onshore in March–April.

The first seasonal peak in juvenile cod abundance at Bellevue occurred in late summer and autumn. This seasonal peak was composed of two periods of increased abundance, one in late August and September and a second in October and November. The August and September period of increased abundance was due primarily to an influx of pelagic 0-group juveniles which first appeared at lengths as small as 25–35 mm SL. The high abundance in October and November was also due to an influx of 0-group cod, but the following differences were noticed in these fish: (i) larger size (~70 mm SL compared with ~40 mm SL in August and September), (ii) lack of pelagic pigmentation (all individuals had a checkerboard pattern of pigmentation), and (iii) a high proportion (~60%) with encysted metacercaria of the digenean *C. lingua* which is typical of fish from nearshore waters. Tupper and Boutilier (1992) also reported two pulses of settlement of 0-group cod in shallow water off Nova Scotia, the first in late June and the second in mid-August. One difference between the two studies is that newly settled 0-group cod (observed by Tup-

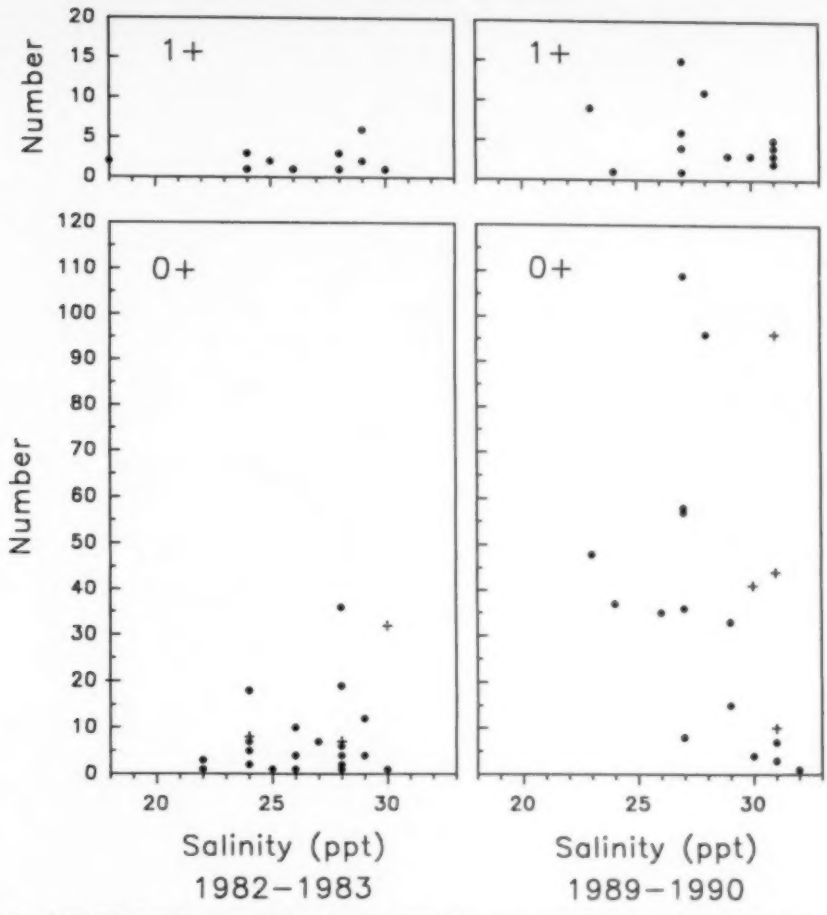

FIG. 8. Number of 0-group and 1-group cod caught in relation to surface (1982–83) and bottom (1.2 m, 1989–90) salinity. Crosses = collections containing pelagic juvenile cod. Only data from nighttime catches are presented.

per and Boutilier 1992) were smaller in mid-August than in June whereas we observed the opposite during the two periods of increased abundance.

Pelagic juveniles first arrive nearshore at Bellevue when temperature and bottom salinity are at or near maximum values (>12°C, >30 ppt). Riley and Parnell (1984) observed that once settled nearshore, 0-group cod (along the English and Welsh coasts) apparently move into regions of lower salinity, with highest catches occurring at salinities of ~20–31 ppt. These authors concluded that cod are found most abundantly at a sequence of water depths, temperatures, and salinities during development to maturity, with depth and salinity generally increasing during ontogeny.

Both the timing and size of nearshore settlement of juvenile cod vary from region to region and there is a suggestion that settlement may occur earlier in shallow nearshore waters as compared with deeper offshore waters both for cod (Daan 1978) and another gadid, *Urophycis tenuis* (Musick 1974). Harden Jones (1968) has summarized the work of Graham and Carruthers (1926) and Corlett (1958) and reported that small cod stay in midwater between 3 and 6 mo after hatching. In the shallow regions of the North Sea, they descend to the bottom within 3–4 mo of hatching (Graham and Carruthers 1926) compared with 4–5 mo when over deeper water. On Georges Bank, cod settle to the bottom at 40–60 mm length (Lough et al. 1989). These are larger than cod collected inshore in this study (25–45 mm SL) and also larger than those observed by Bigelow and Schroeder (1953) (~38 mm) and by Tupper and Boutilier (1992) (~40–50 mm). Pelagic juveniles settle to the bottom primarily during the period June–July to September, with earlier settlement at warmer latitudes (New England, Bigelow and Schroeder 1953; Scotland, Hawkins et al. 1985; Georges Bank, Lough et al. 1989; Nova Scotia, Tupper and Boutilier 1992) and later settlement at more northerly locations (Barents Sea, Bergstad et al. 1987; Iceland, Thorisson 1989). Timing of settlement for juvenile cod from waters off northeast Newfoundland has not been reported but may extend into November.

The second seasonal increase in abundance of juvenile cod occurs in April, May, and June. This increased abundance is concurrent with increases in water temperature (from 3 to 10°C), photoperiod, and with either the melting or departure of land-fast ice. These factors are important

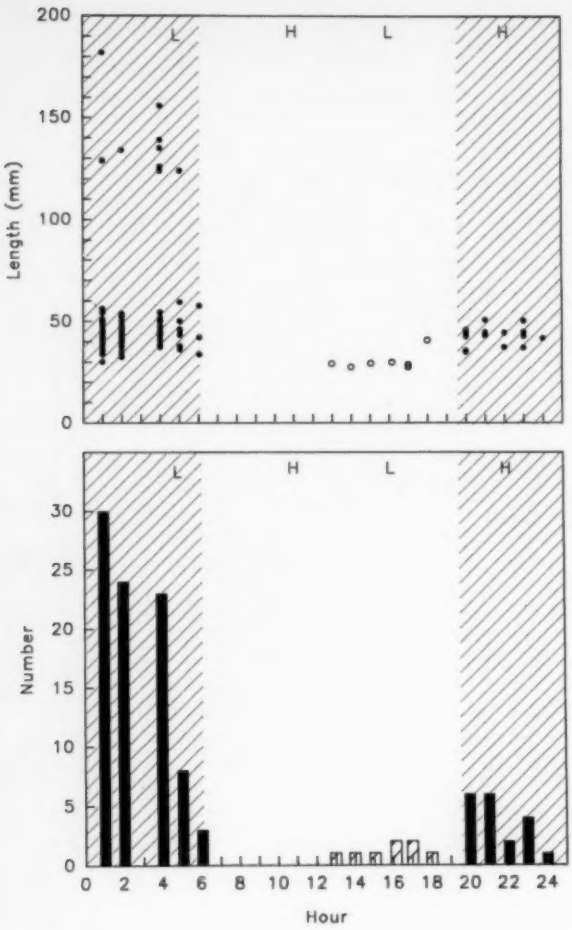

FIG. 9. Diel variation in standard length and number of juvenile cod collected by a small seine over a 24-h period on 21–22 August 1982. Two seinings were conducted each hour. Periods of darkness are shaded. Open and darkened circles and histograms indicate day and night collections, respectively. H = high tide, L = low tide.

for increased productivity that is evident in March and April at Bellevue by the appearance of green algal mats close to shore. Seasonal increases in water temperature, photoperiod, and productivity may be important cues for the inshore movement of small juvenile cod in spring.

Our study has shown that catches of 0-group cod varied by a factor of 2.7 between years. This variation cannot be attributed to differences in fishing gear/methods, substrate, depth, tide, or temperature because these were either held constant throughout the study (gear, methods, habitat, substrate, tide) or were not significantly different (temperature) during the years examined. There are many reasons why the abundance of juvenile cod may vary from year to year. Variation in wind speed and direction, hydrographic conditions, intensity, time, and location of spawning, either inshore (Trinity Bay) or offshore (northeast Newfoundland Shelf), and year-class strength may be important in determining the abundance of 0-group cod inshore. Olsen and Soldal (1989) studied 0-group cod along the coast of Finnmark, northern Norway, and stated "it is conceivable that the coastal abundance is not determined by year-class strength, but rather by the holding capacity" of the nearshore habitat and that this habitat may in general always be fully utilized by juvenile cod regardless of year-class strength. If this hypothesis is correct and applicable to cod occupying coastal regions of Newfoundland, then variation in abundance by a factor of 2.7 between years should be viewed as a relatively small difference. To test Olsen and Soldal's (1989) hypothesis, additional data would have to be collected, preferably during years of low variability in year-class strength, to determine how variable inshore catches of juvenile cod are from year to year. Subsequent sampling along the coast of Finnmark has shown that only limited numbers of 0-group cod were found in nearshore habitats and that these habitats were occupied by large amounts of 1- and 2-yr-old cod, haddock (*Melanogrammus aeglefinus*), and saith (*Pollachius virens*). It is possible that numbers of 0-group cod were reduced in inshore habitats because of competition and predation from these larger fish (A.V. Soldal, personal communication).

The relation between abundance of demersal juvenile cod (collected from both inshore and offshore habitats) and subsequent recruitment to the fishery has been examined in several studies. Some of these reported significant positive correlations with older cod of the same year class (Lear et al. 1980; Ponomarenko 1984; Tveite 1984), while others found no relation (Beacham 1981). Lear et al. (1980) used the average catch per tow, total catch (three best tows), and the highest single catch of 0-group and 1-group cod collected in several bays along the coast of Newfoundland as indices of juvenile abundance. Although significant correlations resulted, indices of abundance were not reflected consistently either in estimates of stock size or in abundance of older cod from the same year-class. Lack of a consistent relationship was believed to be due to large variances associated with biomass surveys for groundfish and to nonstandardized fishing techniques when deploying the beach seine.

A further problem with surveys for demersal 0-group cod as indicators of stock abundance is locating the habitat ("nursery areas") where these cod settle to the bottom in late summer and autumn. Newly settled demersal 0-group cod have been collected at inshore locations (Lear et al. 1980). Yearlings have been collected in numerous offshore habitats including the Grand Bank, off Labrador, off southern Newfoundland, and on the northeast Newfoundland Shelf (Templeman and Fleming 1965; Serebryakov 1968). However, it is not known what proportion of newly settled cod occurs inshore versus offshore and whether this changes from year to year. Olsen and Soldal (1989) estimated that the coastal nursery grounds of Finnmark contribute ~10% of the total brood. This estimate was based on data collected on a poor year-class, when nearshore regions were hypothesized to contribute the most. However, an estimate of 10% may be an underestimate because vessel acoustic transects "frequently could not be extended close enough to the rocky shore to record the innermost border of school aggregations where density was often highest" (Olsen and Soldal 1989).

Lear and Green (1984) suggested that eggs and larvae are carried southward by the Labrador Current and that the coastal bays of northeast Newfoundland are likely nursery areas. This contrasts with the observations of Helbig et al. (1992), who conducted numerical simulations of particle

drift in the surface ocean layer and concluded that the northeast Newfoundland Shelf must be identified as a more likely nursery area for eggs and larvae. Helbig et al. (1992) did not exclude the inshore region as a possible nursery area but concluded that favourable storm tracks were required for significant numbers of eggs and larvae to be transported to the coastal regions of northeast Newfoundland.

It seems likely that other mechanisms in addition to storm events may be involved in the transport of eggs, larvae, and pelagic juvenile cod to coastal areas. This is because the timing of the initial arrival and of the settlement of pelagic juveniles in coastal regions of southern Trinity Bay is relatively consistent (usually during the last 2 wk of August and in September) compared with the randomness that is usually associated with the occurrence, intensity, and direction of storm tracks.

Finally, 0-group cod collected along the coast of Newfoundland may originate from both offshore and inshore spawning populations. If inshore 0-group cod are progeny of discrete (either spatially or temporally) inshore spawning events, then these may be, in part, responsible for the two periods of high abundance observed in August–September and October–November at Bellevue. Further sampling will be required to determine if these two periods of abundance are characteristic of other locations in Newfoundland and if they represent 0-group cod from different spawning events.

Acknowledgements

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Use of Otolith Morphology in Stock Discriminations of Atlantic Salmon (*Salmo salar*)

K.D. Friedland

National Marine Fisheries Service, Woods Hole Laboratory, Woods Hole, MA 02543, USA

and D.G. Reddin

Department of Fisheries and Oceans, Science Branch, P.O. Box 5667 St. John's, NF A1C 5X1, Canada

Friedland, K.D., and D.G. Reddin. 1994. Use of otolith morphology in stock discriminations of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 51: 91–98.

Shape of sagittal otoliths was used to develop discriminant function models to classify Atlantic salmon (*Salmo salar*) by continent and country of origin. The outline shape was digitized with an image processor and used to calculate a complex Fourier transform of the closed contour and two shape indices, rectangularity and circularity. The shape indices and the magnitudes of the first 20 nonzero or nonidentity harmonics were used as input variables. Samples were obtained from known-origin one-sea-winter salmon captured in either Canada or West Greenland during 1986–88. Classification by continent of origin was designed to discriminate between North American and European salmon. Jackknifed classification efficiency was 88% for the continent model. Classification by country of origin was designed to discriminate between salmon of United States and Canada origin and between salmon of Ireland and United Kingdom origin; these models performed with classification efficiencies of 64 and 69%, respectively. These results suggest that otolith morphology may be an effective tool to identify continent of origin for salmon fisheries management. However, before the model is implemented, the discriminant function training set should be broadened to include a wider cross section of stocks likely to occur in mixed-stock fisheries.

La forme des sagitta des otolithes a servi à élaborer des modèles de fonction discriminante permettant de classer les saumons atlantiques (*Salmo salar*) selon le continent et le pays d'origine. Le contour extérieur a été numérisé avec un processeur d'images et a servi à calculer une transformée de Fourier complexe du contour fermé et deux indices de forme, la rectangularité et la circularité. Les indices de forme et la grandeur des 20 premières harmoniques d'ordre non-zéro de non-identité ont servi de variables d'entrée. On a obtenu des échantillons d'origine connue de saumons unibermarins capturés soit au Canada soit à l'ouest du Groenland en 1986–1988. La classification par continent d'origine a été conçue pour distinguer entre le saumon nord-américain et le saumon européen. L'efficacité de la classification selon la technique du « canif » était de 88 % pour le modèle de l'origine continentale. La classification par pays d'origine a été conçue pour distinguer entre les saumons des États-Unis et du Canada, et entre les saumons provenant d'Irlande et du Royaume-Uni; ces modèles n'ont pas donné de bons résultats, l'efficacité de classification étant respectivement de 64 et 69 %. Ces résultats semblent indiquer que la morphologie des otolithes peut constituer un outil efficace pour identifier le continent d'origine dans la gestion des pêcheries de saumon. Toutefois, avant de mettre en oeuvre le modèle, il serait nécessaire d'élargir la base d'apprentissage de l'analyse discriminante pour y faire entrer un échantillonnage plus vaste des stocks susceptibles de se retrouver dans les pêcheries mixtes.

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Crucial to the assessment of Atlantic salmon (*Salmo salar*) stocks in the North Atlantic is the ability to identify salmon caught in various commercial fisheries by their country or continent of origin (Reddin et al. 1988). A variety of approaches have shown varying degrees of usefulness when their accuracy and effectiveness within the constraints of fishery sampling programs are considered. Attempts have been made to classify salmon by means of their parasites (Pippy 1980), genetic markers (Nyman and Pippy 1972; Child et al. 1976; Child 1980; Payne 1980; Davidson et al. 1989; Hovey et al. 1989; Bermingham et al. 1991; Cutler et al. 1991), and morphology (MacCrimmon and Claytor 1985, 1986; de Pontual and Prouzet 1987, 1988). None of these methods proved to be particularly effective due to difficulties encountered in collecting samples or because of unacceptable classification accuracy.

The classification techniques best suited to North Atlantic salmon fisheries have been those based on scale characteristics (Lear and Sandeman 1980; Reddin 1986; de Pontual and Prouzet 1987, 1988; Reddin et al. 1992). In these techniques, salmon captured at sea, for example in the West Greenland salmon fishery, are allocated to continent of origin, either North America or Europe, on the basis of circuli counts. Because scales are easy to collect and are used for age determination, their secondary use to identify stock membership is both logical and efficient. However, the key characters used in the scale-based classification models are subject to interannual variation. Consequently, new train-

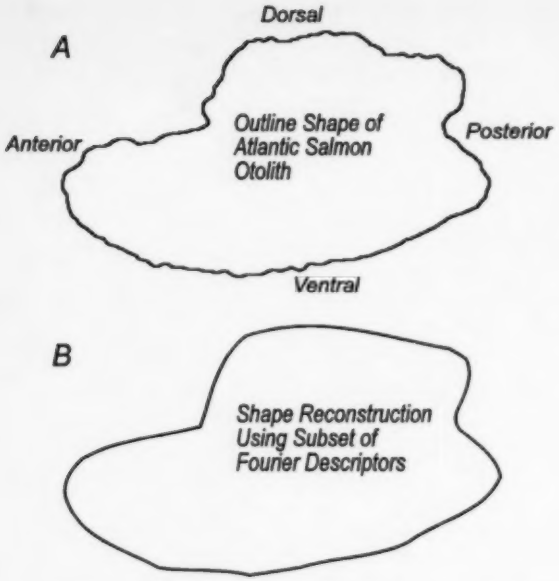


FIG. 1. (A) Atlantic salmon otolith outline shape in the standard orientation used in this study. (B) Otolith outline shape formed with a reverse Fourier transform of the outline in Fig. 1A using only the first 15 harmonics of the transform.

ing sets must be compiled each year which are identified to their continent of origin by other means (Reddin et al. 1990). Genetic markers have been used to develop these training sets, but not without the difficulty of collecting tissue samples in remote areas and their less than complete classification efficiency (Verspoor 1986). Clearly, there is a need to improve the methods used to identify continent of origin of Atlantic salmon and if possible increase resolution to country of origin.

The morphological and meristic characters of a number of hard body parts of fish have been useful in stock identification studies both in freshwater and marine contexts. In particular, simple otolith morphometrics have been used to identify anadromous versus nonanadromous spawning components of salmon populations, to identify juvenile stages of closely allied species, and to classically define stock structure (Messieh 1972; Currens et al. 1988; L'Abée-Lund 1988). More complex measurements involving the decomposition of otolith shape into its Fourier descriptors have been used to identify a wide range of stock structures (Casselman et al. 1981; Riley and Carline 1982; Bird et al. 1986; Castonguay et al. 1991) since the approach was first introduced by Jarvis et al. (1978). The purpose of this paper is to examine the performance of shape characteristics of Atlantic salmon otoliths in models to discriminate continent and country of origin, for use in the West Greenland and other fisheries.

Materials and Methods

Sagittal otolith samples were collected from one-sea-winter (1SW) coded wire and Carlin tagged salmon captured in West Greenland waters during 1986, 1987, and 1988 and in Canada during 1987 and 1988. Otoliths were carefully dissected from the salmon and placed in vials without preservative or allowed to air-dry in scale envelopes. In the laboratory, the otoliths were soaked in water to elute any residual soft tissue for removal. Because both otoliths were not always available due to loss during dissection or breakage, either member of the otolith pair was used. Otolith orientation was standardized by positioning the anterior end of the otolith to the reader's left (Fig. 1A). By noting whether the sulcul groove was up or down, the reader was able to identify right- from left-side otoliths (referenced in tables and graphs as 1 for right and 2 for left).

A complex Fourier transform of otolith outline shape and two shape indices were collected for each otolith using a Biosonics image analysis system.[1] A complex Fourier shape analysis requires that a closed contour of the shape (here the otolith) be developed in a complex coordinate space. This is accomplished by taking equally spaced coordinates along the perimeter of the otolith; these coordinates can be modelled as a closed periodic function:

$$(1) \quad U(t) = X(t) + iY(t)$$

where $i = \sqrt{-1}$, X and Y are Cartesian coordinates, and t is the path length with the period T equal to the perimeter. Because the function is periodic, it can be expressed as a Fourier series, or for computational purposes as a truncated Fourier series. The solution is a series of Fourier coefficients which are complex numbers. The solution set was calculated by an implementation of the algorithm of Wallace and Wintz (1980) (Biosonics 1987). For the discriminant analysis the magnitude of the harmonics was calculated as

$$(2) \quad \text{Magnitude} = \sqrt{(\text{real}^2 + \text{imaginary}^2)}$$

where real and imaginary are the parts of each coefficient. The higher the number of harmonics included in the model, the closer the fit to the original shape. The salient features of otolith shape appeared to be captured with the first 15–20 harmonics (Fig. 1B). The periodogram was then normalized for position and size by setting the zero frequency component to zero and dividing the amplitude coefficients by the value for the first component, respectively (Wallace and Wintz 1980). Only the first 20 nonzero and nonidentity magnitudes were used in the analysis. In addition to the magnitudes of the Fourier transform, two information indices were used as variables for discriminant analysis: rectangularity, defined as the otolith area divided by the area of its minimum enclosing rectangle, and circularity, defined as the perimeter squared divided by the area. Distributions of all variables were tested for normality with the Kolmogorov–Smirnov one-sample goodness-of-fit test. The rectangularity index was normalized with an arcsin transformation.

The database of otolith shape descriptors consisted of data from 471 otoliths collected from 12 stock groups (Table 1). The North American otoliths were from salmon originating in at least 12 rivers. United States origin otoliths were predominantly from the Penobscot River in Maine. Canadian-origin otoliths were predominantly from rivers in the provinces of Nova Scotia and New Brunswick including the Tusket, Medway, North, Margaree, and Saint John. European-origin otoliths were from at least 21 rivers, mostly from rivers in Ireland, England, and Wales. Many of United Kingdom origin otoliths were from wild salmon marked as

[1]Reference to tradenames does not imply endorsement.

TABLE 1. Stock composition of Atlantic salmon otolith database. Totals are for both right and left otoliths.

Stock group	Contributing rivers	Number of otoliths
North America		
U.S. (Maine)	Penobscot	218
U.S. (Connecticut)	Connecticut	8
U.S. (Massachusetts)	Merrimack	9
Canada (Nova Scotia)	Tusket, Medway, North, Margaree	32
Canada (Prince Edward Island)	Morrell	6
Canada (New Brunswick)	Nepisiquit, Kedgwick, Miramichi, St. John	15
Canada (unknown)		47
North America (unknown)		7
North America subtotal		342
Europe		
Ireland	Corrib, Lee, Erne, Shannon, Virginia, Screebe, Shalle, Ballyshannon, Lock Furnace, Castleconnell	72
U.K. (England and Wales)	Tyne, Ware, Tees, Thames, Coquet, Usk, Tavy	39
U.K. (Scotland)	Lussa	5
France	Unknown	3
Iceland	Kollafjördur, Laxa-i-Ting	8
Norway	Imsa	2
Europe subtotal		129
Database total		471

parr in tagging programs in England, resulting in low returns for many river systems. Otolith collections were not evenly distributed over years; contributions to the database were 6, 58, and 36% for 1986, 1987, and 1988, respectively. The proportion of right and left otoliths in the database was 50% for both continents.

Continent, year, and otolith pair member (right versus left otolith) effects on otolith shape were compared by MANOVA. The first MANOVA comparison tested the effect of continent with rectangularity, circularity, and the magnitudes of the first 20 nonzero or nonidentity harmonics as dependent variables. Year and pair member effects were evaluated by continent with the same set of dependent variables used in the continent comparison.

Discriminant function models were constructed using rectangularity, circularity, and magnitude data. Three discriminant functions were developed: (1) North American and European continent of origin using both right- and left-side otoliths, (2) United States and Canada country of origin using both right- and left-side otoliths, and (3) Ireland and United Kingdom country of origin using both right- and left-side otoliths. Stepwise linear discriminant analysis, using forward and backward stepping, was used to guide selection of variable sets used in each function (SAS 1990). The number of variables used was constrained at 22, conservatively below the limits suggested by Saila and Martin (1987). Homogeneity of the within-group covariance matrices was tested and either a linear (matrices are homogenous and the pooled matrix is used) or a quadratic (matrices are not homogenous and individual within-group matrices are used) discriminant function was computed (SAS 1990). Because of the widely disparate sample sizes between groups, comparisons were performed with all the samples of the less numerous group and a series of random draws from the other group. The functions for five draws are presented. Prior probability of classification was equal for both groups. Classification efficiency (percent correctly classified) were cross-validated estimates according to the methods of Lachenbruch and Mickey (1968). Cohen's kappa (κ) statistic and its 95% confidence interval were computed for each discriminant function (Titus et al. 1984). This statistic estimates the improvement over chance of the percent corrected classification rates.

Results

The median and dispersion patterns of Fourier transform coefficients for North American and European otoliths, using both right and left otoliths, indicate some utility of these shape descriptors for discriminating stock origin (Fig. 2). The greatest spectral density is contained in the coefficients for harmonics 1–5 and gradually decreases with the higher order harmonics. There is a great deal of overlap in 25th and 75th percentile ranges (box plot range) for the coefficients of most harmonics between North American and European salmon. For the comparison of North American and European stocks the greatest differences can be seen in harmonics 4 and 6. The medians of Fourier transform coefficients are not presented for the comparison of North American and European otoliths sorted by right and left otoliths, coeffi-

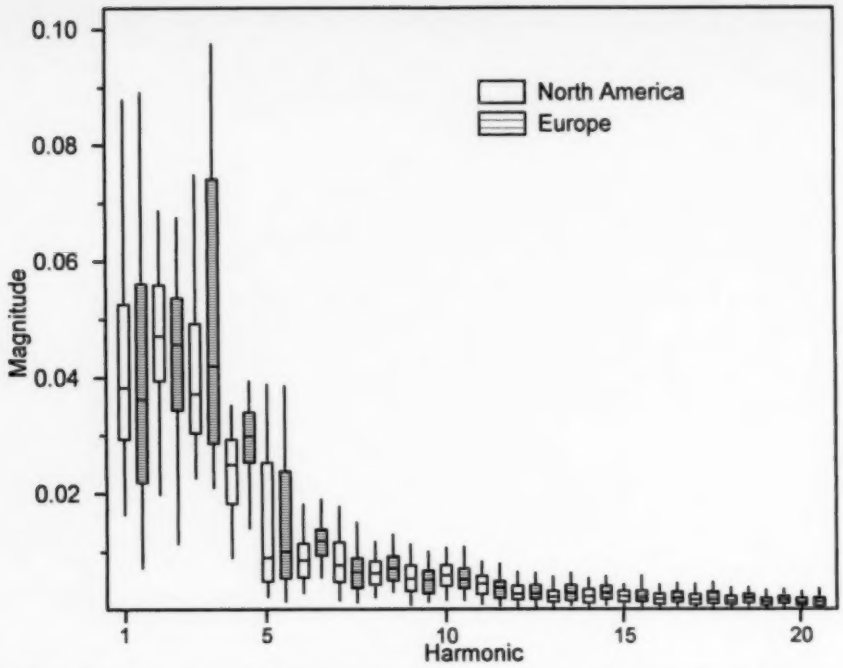


FIG. 2. Box plots of Fourier transform magnitudes of harmonics 1–20 for North American and European otoliths.

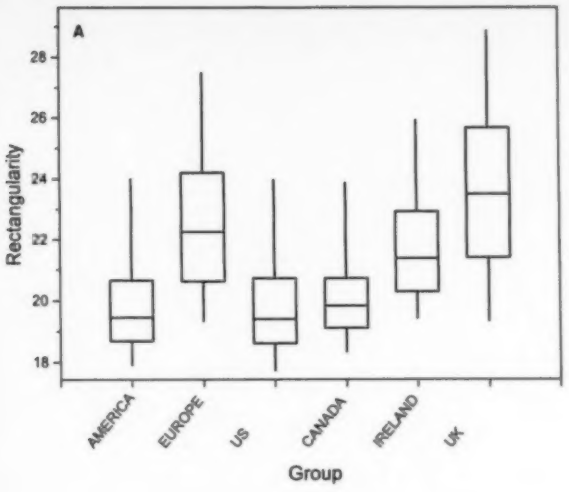
cients sorted by year, or for comparisons by country using otoliths from the United States and Canada and Ireland and the United Kingdom. As with the example presented for North American and European otoliths, spectral density is similarly distributed among harmonics and there is overlap for most harmonics pairs between groups.

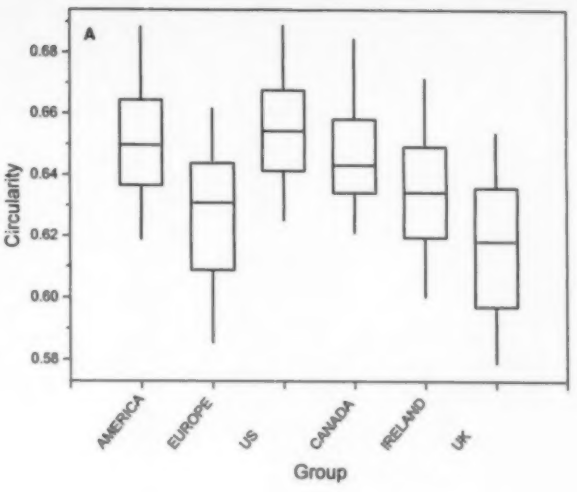
The median and dispersion patterns for the rectangularity indices were compared between continents and countries and between right and left otoliths and year within continent. The box plot ranges for North American and European otoliths were essentially nonoverlapping whereas comparisons between countries (United States and Canada and Ireland and the United Kingdom) showed great overlap (Fig. 3A). Rectangularity indices for North American stocks were generally between 19 and 21 whereas European otoliths had rectangularity indices between 21 and 24. The box plot ranges for right and left otoliths within continent were similar as were the ranges for indices sorted by year (Fig. 3B).

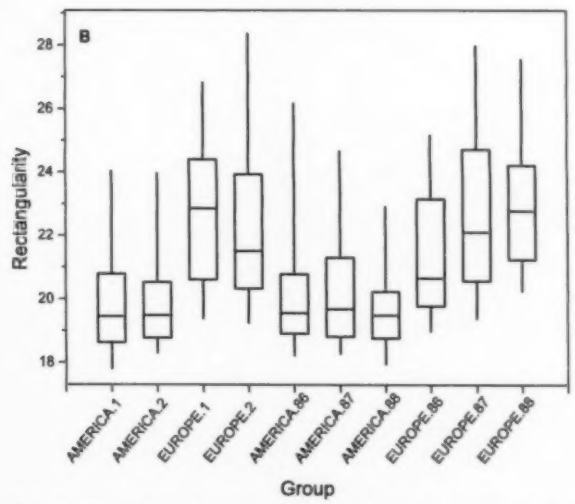
The median and dispersion patterns of the circularity indices were compared between continents and countries and between right and left otoliths and year within continent. The box plot ranges for North American and European otoliths did not overlap whereas comparisons between country (United States and Canada and Ireland and the United Kingdom) showed moderate overlap (Fig. 4A). North America otoliths had circularity indices generally ranging from 0.64 to 0.66 whereas the European otoliths and circularity indices generally ranging from 0.63 to 0.64. The box plot ranges for right and left otoliths within continent were similar as were the ranges for indices sorted by year (Fig. 4B).

The continent effect on otolith shape data was highly significant (MANOVA, $F = 20.61$, $P < 0.001$) whereas the year effect (North America: $F = 1.37$, $P = 0.127$; Europe: $F = 1.10$, $P = 0.354$) and the pair member effect (North America: $F = 1.13$, $P = 0.310$, Europe: $F = 0.984$, $P = 0.490$) comparisons were not significant.

The discriminant function developed to identify continent of origin classified otoliths more efficiently than functions to identify country of origin. The discriminant function to identify continent of origin (using both right and left otoliths) had an average classification efficiency of approximately 88% (Table 2). The function was formed with the rectangularity and circularity indices and the magnitude variables M1, M3, M4, M6, M7, M11, M13, M16, and M19. Between-group classification bias ranged between ±0.0 and ±3.1%. Cohen's κ indicated that the classification efficiency was approximately 75% better than would have occurred by chance alone. The discriminant function to identify country of origin (United States and Canada and Ireland and the United Kingdom) using both right and left otoliths had average classification efficiencies of approximately 64 and 69%, respectively (Tables 3 and 4). The United States – Canada function was formed with the rectangularity and circularity indices and the magnitude variables M1, M3, M4, M5, M8, M9, M10, M19, and M20. Between-group classification bias ranged between ±0.0 and ±7.0%. Cohen's κ indicated that the classification efficiency was approximately 28% better than would have occurred by chance alone. The Ireland – United Kingdom function was formed with the magnitude variables M6, M10, M11, M16, and M19. Between-group classification bias ranged between ±1.1 and ±4.5%. Cohen's κ indicated that the classification efficiency was approximately 36% better than would have occurred by chance alone. Magnitude variables M1, M3, M4, M6, M7, M10, M11, M13,







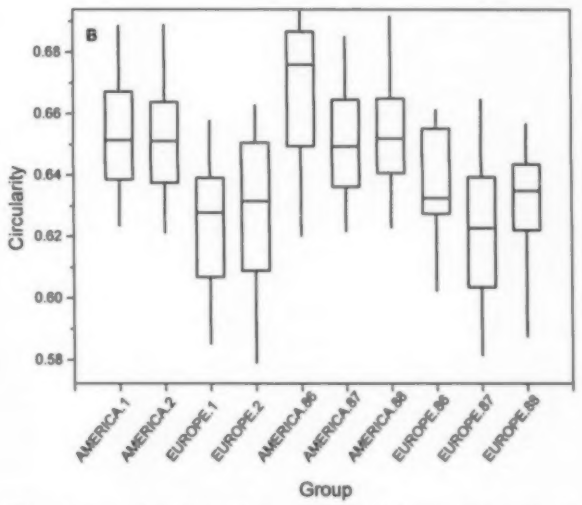


FIG. 3. Box plot of rectangularity indices (A) by continent (North America and Europe) and country (United States and Canada and Ireland and the United Kingdom) using data for right and left otoliths and (B) by otolith pair member (1, right; 2, left) and by year (1986, 1987, and 1988) for North America and Europe.

FIG. 4. Box plot of circularity indices (A) by continent (North America and Europe) and country (United States and Canada and Ireland and the United Kingdom) using data for right and left otoliths and (B) by otolith pair member (1, right; 2, left) and by year (1986, 1987, and 1988) for North America and Europe.

M16, and M19 were common to two or more of the discriminant functions developed whereas variables M13 and M20 were unique to one function.

Discussion

Otoliths of Atlantic salmon of North American and European origin appear to have distinctive shapes and could potentially be useful in the procedures used to develop estimates of catch by continent of origin in the West Greenland fishery. Otoliths, although easier to collect and preserve than the types of tissue samples used in biochemical stock identification techniques, are in turn less adaptable to a fishery-wide sampling program than scales because they are more difficult and time consuming to collect. In addition, adult otoliths cannot be readily adapted to freshwater age determinations, a task which is easily accomplished with scales. Thus, the potential use of otoliths would be to identify salmon to continent so their scales could be used as a training set for scale-based stock identification models (Reddin et al. 1990). Before this procedure could be implemented, concerns about the inclusion of misidentified scales in the training set, which would occur if the otolith model were used in its present state, must be satisfied. Undoubtedly, errors in the training data sets developed from otoliths would be carried forward and result in large errors in the scale-based stock identification model, so the continental catch trend data generated from it would be problematic.

The refinement with the highest priority would be to retrain the otolith model with a collection of randomly selected

TABLE 2. Quadratic discriminant function models to classify Atlantic salmon to continent (North America or Europe) of origin. Model variables include rectangularity, circularity, and M1, M3, M4, M6, M7, M11, M13, M16, and M19. Each trial is based on all European samples and a random draw of North American samples.

Trial	Group	*N*	Cross-validated percent correct	Group bias (%)	Cohen's	κ
1	North America	129	89.2	0.0	Lower 95% CI	0.705
	Europe	129	89.2	0.0	κ	0.783
	Total		89.2		Upper 95% CI	0.860
2	North America	129	89.9	3.1	Lower 95% CI	0.652
	Europe	129	83.7	−3.1	κ	0.736
	Total		86.8		Upper 95% CI	0.821
3	North Amecia	129	90.7	2.7	Lower 95% CI	0.679
	Europe	129	85.3	−2.7	κ	0.760
	Total		88.0		Upper 95% CI	0.841
4	North America	129	90.7	2.7	Lower 95% CI	0.679
	Europe	129	85.3	−2.7	κ	0.760
	Total		88.0		Upper 95% CI	0.841
5	North America	129	87.6	1.9	Lower 95% CI	0.626
	Europe	129	83.7	−1.9	κ	0.713
	Total		85.7		Upper 95% CI	0.800
	Mean		87.5		Lower 95% CI	0.668
					κ	0.750
					Upper 95% CI	0.833

TABLE 3. Quadratic discriminant function models to classify Atlantic salmon to country (United States or Canada) of origin. Model variables include rectangularity, circularity, and M1, M3, M4, M5, M8, M9, M10, M11, M18, M19, and M20. Each trial is based on all Canadian samples and a random draw of United States samples.

Trial	Group	*N*	Cross-validated percent correct	Group bias (%)	Cohen's	κ
1	United States	100	55.0	−7.0	Lower 95% CI	0.103
	Canada	100	69.0	7.0	κ	0.240
	Total		62.0		Upper 95% CI	0.377
2	United States	100	57.0	−5.0	Lower 95% CI	0.103
	Canada	100	67.0	5.0	κ	0.240
	Total		62.0		Upper 95% CI	0.377
3	United States	100	66.0	0.0	Lower 95% CI	0.186
	Canada	100	66.0	0.0	κ	0.320
	Total		66.0		Upper 95% CI	0.454
4	United States	100	60.0	−3.5	Lower 95% CI	0.134
	Canada	100	67.0	3.5	κ	0.270
	Total		63.5		Upper 95% CI	0.406
5	United States	100	67.0	1.0	Lower 95% CI	0.186
	Canada	100	65.0	−1.0	κ	0.320
	Total		66.0		Upper 95% CI	0.454
	Mean		63.9		Lower 95% CI	0.142
					κ	0.278
					Upper 95% CI	0.414

otoliths from the West Greenland fishery. Our training set is biased toward a group of marked stocks which may or may not reflect the hundreds of stocks composing each continental stock complex. To assemble a training set appropriate for the West Greenland fishery, we will have to identify by other means unmarked 1SW salmon caught in West Greenland waters, most likely by a genetic technique (Cutler et al. 1991). Samples of salmon otoliths collected in homewaters would not be appropriate due to the expected differences in otolith shape of salmon of different age or size (de Pontual et al. 1983; Smith 1992).

A remidal measure to allow use of the otolith-based stock identification models in the procedure to classify West Greenland catch by continent would be simply to change

TABLE 4. Linear discriminant function models to classify Atlantic salmon to country (Ireland or United Kingdom) of origin. Model variables include M6, M10, M11, M16, and M19. Each trial is based on all U.K. samples and a random draw of Irish samples.

Trial	Group	*N*	Cross-validated percent correct	Group bias (%)	Cohen's	κ
1	Ireland	44	75.0	2.3	Lower 95% CI	0.265
	United Kingdom	44	70.4	−2.3	κ	0.455
	Total		72.7		Upper 95% CI	0.644
2	Ireland	44	63.6	−2.3	Lower 95% CI	0.116
	United Kingdom	44	68.2	2.3	κ	0.318
	Total		65.9		Upper 95% CI	0.520
3	Ireland	44	72.7	−4.5	Lower 95% CI	0.165
	United Kingdom	44	63.6	4.5	κ	0.364
	Total		68.2		Upper 95% CI	0.562
4	Ireland	44	72.7	−4.5	Lower 95% CI	0.165
	United Kingdom	44	63.6	4.5	κ	0.364
	Total		68.2		Upper 95% CI	0.562
5	Ireland	44	68.2	1.1	Lower 95% CI	0.116
	United Kingdom	44	70.4	−1.1	κ	0.318
	Total		69.3		Upper 95% CI	0.520
	Mean		68.9		Lower 95% CI	0.165
					κ	0.364
					Upper 95% CI	0.562

the evaluation criteria of posterior probabilities for unknown samples. Unknown samples would be allocated to either continent or a third group with intermediary characters that would not be classified. An important control on this procedure would be to evaluate the composition of samples likely to be unclassified. If stock groups which are important contributors to the fishery are excluded, the approach may be biased.

We encourage the testing of models of mixed data types as a means of improving classification efficiency. Our model is relatively simple in that it relies exclusively on information from otolith outline shape. Studies by MacCrimmon and Claytor (1985, 1986), de Pontual and Prouzet (1987, 1988), and Reddin et al. (1992) suggest that data based on other traits, which are also relatively easy to collect, may be useful in identifying continent of origin. Although not available for testing in our study, future model construction should explore mixed data type models, i.e., based on otolith shape, scale shape, and body shape.

The lack of demonstrable differences in shape of right and left otoliths suggests that future work can disregard which member of the otolith pair is removed. This is not trivial because in the field, it is common to recover only one otolith successfully from an individual fish. Collection of two otoliths would permit two determinations of continent of origin for that individual.

Otolith shape appears to be a weak tool for identification of country of origin. Our limited trials with models designed to classify salmon originating from neighboring countries performed too poorly to implement. Genetic differences (Child et al. 1976; Hovey et al. 1989) have been demonstrated for river stocks in close proximity to each other. Likewise, shape factors for scales (de Pontual and Prouzet 1987) were different for stocks from neighboring countries. Also, there are racial differences between stocks and stock groups within continent which could be useful to identify samples to stock origin for management proposes. Whether otolith shape would be useful in country or regional stock identification models is equivocal and we encourage further testing of otolith shape data to discriminate stocks and stock groups.

We are quite confident of the differences in otolith shape for the North American versus European salmon we analyzed, but what is not clear to us is whether these phenotypic differences are genetically or environmentally induced. Morphological techniques for identification of Atlantic salmon continent of origin are based on environmentally influenced characters. These characters have been relatively stable over time because they depend on difference in postsmolt habitats of the respective continental groups (Reddin 1986). We know that these methods and others based on morphological traits are subject to significant annual and regional variation (Lear and Misra 1978; Blouw et al. 1988). On the other hand, otolith morphology is commonly used as a species-level character in fish systematics; thus, the pattern of phenotypic expression is considered similar to other calcified structures (Lagler et al. 1977). However, recent work has demonstrated that otolith morphology can vary in response to differences in growth regimes for a range of species (Reznick et al. 1989; Secor and Dean 1989; Smith 1992). We found no difference in the shape of otoliths between the two years sampled. It is interesting to note that the scale character circuli number during the first sea-winter, which is used to identify continent of origin of Atlantic salmon, was different for the same two years for the winter-based character ($F = 42.8$, $P < 0.001$) but not for the summer-based character ($F = 0.26$, $P = 0.61$) (P.G. Reddin, unpublished data). This limited comparison suggests that the greater influence on otolith shape may be genetic.

In summary, we have demonstrated that otolith shape can be useful to discriminate origin of Atlantic salmon caught in mixed-stock fisheries to continent of origin. It is suggested

that if the shape of otoliths in salmon is not environmentally influenced, otoliths may be used to annually define a database of known-origin salmon scales that could be used to identify continent of origin based on the analysis of scales.

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Determination of Composition and Vertical Structure of Fish Communities Using in situ Measurements of Acoustic Target Strength

M. Barange, I. Hampton, S.C. Pillar and M.A. Soule

Sea Fisheries Research Institute, Private Bag X2, 8012 Rogge Bay, Republic of South Africa

Barange, M., I. Hampton, S.C. Pillar, and M.A. Soule. 1994. Determination of composition and vertical structure of fish communities using in situ measurements of acoustic target strength. Can. J. Fish. Aquat. Sci. 51: 99–109.

A split-beam echo-sounder was used to estimate in situ acoustic target strengths (TS) of fish from a number of different fish communities on the South African continental shelf. The TS and size distributions (obtained by aimed trawling) were used to describe the size structure and vertical distribution of these communities. TS distributions obtained from several monospecific populations of juvenile Cape hake (*Merluccius capensis*), the dominant species present, were self-consistent, and there was good correspondence between modes in the TS and length distributions of juvenile hake, adult round herring (*Etrumeus whiteheadi*), anchovy (*Engraulis capensis*) recruits, pelagic goby (*Sufflogobius bibarbatus*), horse mackerel (*Trachurus trachurus capensis*), and ribbon fish (*Lepidopus caudatus*). Average TS values for all these species, both per individual and normalized by weight, are presented and compared with published values. The use of TS information in studies of the small-scale community structure and dynamics of fish populations is discussed. It is concluded that the method can be effective on low-density, multispecific assemblages such as those in our study, avoiding many of the pitfalls of conventional net sampling.

Un échosondeur à faisceau partagé a été utilisé pour estimer in situ les intensités de cible acoustique (TS) des poissons dans un certain nombre de différentes communautés sur le plateau continental de l'Afrique du Sud. Les distributions des TS et des tailles (obtenues par chalutage contrôlé) ont servi à décrire la structure des tailles et la distribution verticale de ces communautés. Les distributions des TS obtenues à partir de plusieurs populations monospécifiques de juvéniles de merlu du Cap (*Merluccius capensis*), la principale espèce présente, étaient cohérentes, et on observait une bonne correspondance entre les modes des distributions des TS et des longueurs chez les merlus juvéniles, les shadines adultes (*Etrumeus whiteheadi*), les recrues d'anchois du Cap (*Engraulis capensis*), le gobie pélagique (*Sufflogobius bibarbatus*), le chinchard du Cap (*Trachurus trachurus capensis*) et le sabre argenté (*Lepidopus caudatus*). Les valeurs moyennes des TS pour toutes ces espèces, aussi bien pour les individus qu'après normalisation par poids, sont présentées et comparées aux données publiées. Nous analysons l'utilisation de l'information sur les TS dans les études sur la structure à petite échelle des communautés et la dynamique des populations de poissons. Nous en concluons que la méthode peut être efficace pour des assemblages plurispécifiques à faible densité comme ceux de notre étude, et qu'elle permet d'éviter les écueils de l'échantillonnage classique au filet.

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Echo-integration has become a widespread acoustic technique to estimate the size of commercially important fish stocks (e.g. Karp 1990; MacLennan and Simmonds 1992). Accuracy, however, depends on the precision of target strength (TS) estimates used in converting measurements of acoustic scattering intensity to estimates of fish biomass. During the last two decades, much effort has been focused on refining techniques to improve the accuracy of TS estimates, resulting in the development of dual-beam and split-beam transducers (Ehrenberg 1983) to determine the position of single targets in the beam and thereby obtain direct in situ TS estimates from the strength of the echo and knowledge of the transducer directivity. These new improvements provide a better appraisal of spatial and temporal variability than does net sampling, in which deficiencies in sampling fish communities representatively are well recognized (e.g., Walsh 1991; Engås and Soldal 1992; MacLennan 1992). As such, they offer new perspectives into the study of the small-scale structure of fish communities (e.g., Burczynski and Johnson 1986; Rudstam et al. 1987; Jacobson et al. 1990; Boudreau 1992).

TS is related to fish size (e.g., MacLennan and Simmonds 1992) and can be strongly affected by behaviour and physiological state (e.g., Blaxter and Batty 1990; Dawson and Karp 1990; MacLennan et al. 1990; Ona 1990a). Consequently, it is a highly variable parameter that, together with the fact that TS studies have been restricted largely to commercially important species, has limited the use of TS information to studies on monospecific populations (e.g., Traynor and Williamson 1983; Williamson and Traynor 1984; Foote et al. 1986; Foote and Traynor 1988). Nevertheless, it has been proposed that it is possible to interpret TS differences

in terms of differences in fish size (Dickie et al. 1983), suggesting that ecological studies of multispecific assemblages could benefit from the analysis of echo returns (e.g., Lindem 1983; Forbes 1985; Burczynski and Johnson 1986; MacLennan and Forbes 1987; Rudstam et al. 1987; Jacobson et al. 1990). If so, techniques of determining TS accurately (Thiebaux et al. 1991) would have the potential to address questions involving the behaviour and microstructure of fish at the population and community level. The need for such an approach has become increasingly clear, as there is growing evidence that fish communities are not randomly organized but are highly structured assemblages (e.g., Jackson et al. 1992) consisting of populations interacting at several scales (Crowder 1990).

In the present paper, we use TS information from a split-beam echo-sounder to analyze size, relative composition, abundance, and vertical structure of fish assemblages. We examine the hypothesis that, in simple communities under conditions of low species diversity, well segregated by size, the distribution of TS reflects the size composition of the community. If there are few overlapping echoes, the method will also provide an estimate of the relative abundance of each species, based on the target counts. The application of such developments to the study of small-scale fish community structure and behaviour at the individual and population levels is discussed.

Material and Methods

Sampling Strategy

Data were collected onboard F.R.S. *Africana* during February 1992 in nearshore waters (80–110 m depth) off the west coast of South Africa. The region between 29°S and 32°S was chosen because it is a known recruitment area for monospecific, nonshoaling populations of juvenile shallow-water Cape hake (*Merluccius capensis*) suitable for the study. Such conditions were required to ensure an adequate number of nonoverlapping echoes for in situ TS determination. In order to ensure a suitable spread of fish throughout the water column, data were collected only at night, when juvenile hake rise off the bottom (Pillar and Barange 1993).

Areas of study were selected according to the acoustic properties of fish communities, as recorded in echo-charts obtained daily at dawn. Sampling procedure was as follows. Temperature and salinity profiles were first obtained with a Neil Brown Mark III CTD. Fish sampling followed, using an aimed Engels 308 midwater trawl fitted with an 8-mm-mesh codend liner. The net was trawled at approximately 3 kn for 15–30 min. Several trawls were conducted at different depths over fixed transects to cover the entire water column. The transects were generally parallel to the isobaths and typically between 1 and 2 nautical miles long. While trawling, TS data were collected from the depth interval sampled by the net. Relative fish abundance was estimated from the ratio between the number of single identified targets and the number of acoustic transmissions ("pings"). Although it was originally intended to estimate abundance by echo-integration, this was prevented by failure of the echo-integrator during the cruise. Generally, four or five midwater trawls and TS experiments were carried out per night on each selected fish community. On occasion, TS data were collected from the entire water column independently of the depth intervals sampled by the net. In addition, bottom trawls were occasionally conducted to establish the composition of the nonmigrant population when considered necessary.

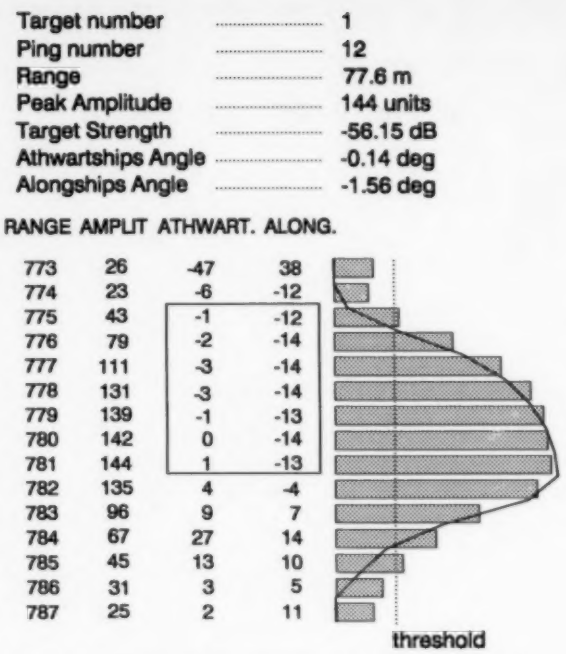

FIG. 1. ES400 parallel output data from a depth layer, 77.3–78.7 m, containing one well-defined fish echo. Threshold set at 40 units. Superimposed line denotes shape of the echo of a calibration sphere, normalized in amplitude to fish echo. Box indicates region of phase lock. Phase readings in columns are in electrical units (1 unit = 0.13°).

All fish collected in the trawls were measured to the nearest centimetre and classified to species level to produce size frequencies of the communities under study. Acoustic data were analyzed as decribed in the following section.

Acoustic Measurements

TS data were obtained from a Simrad ES400 (38-kHz) echo-sounder, using a Simrad ES-38 split-beam transducer (directivity index 29 dB, nominal beamwidth 8.0° between half-power points) fired by a Simrad EK400 transmitter using a 1.0-ms pulse. A month after the cruise the system was calibrated to within an estimated 0.5 dB with a 60-mm copper sphere according to procedures set out in Foote et al. (1987). Pertinent parameters measured were the combined source level and voltage response and the half-power points of the beam. The latter were obtained by moving the transducer relative to the sphere and plotting sphere amplitude against angular bearing.

Target amplitude, range, and bearing, both alongships and athwartships, were sampled from the parallel port of the ES400 at 0.133-ms intervals (corresponding to depth intervals of 0.1 m) by an IBM-compatible AT computer. The range, peak amplitude, and bearings of an echo were stored if (a) the peak fell within the depth range of interest and exceeded a threshold set marginally above the noise level

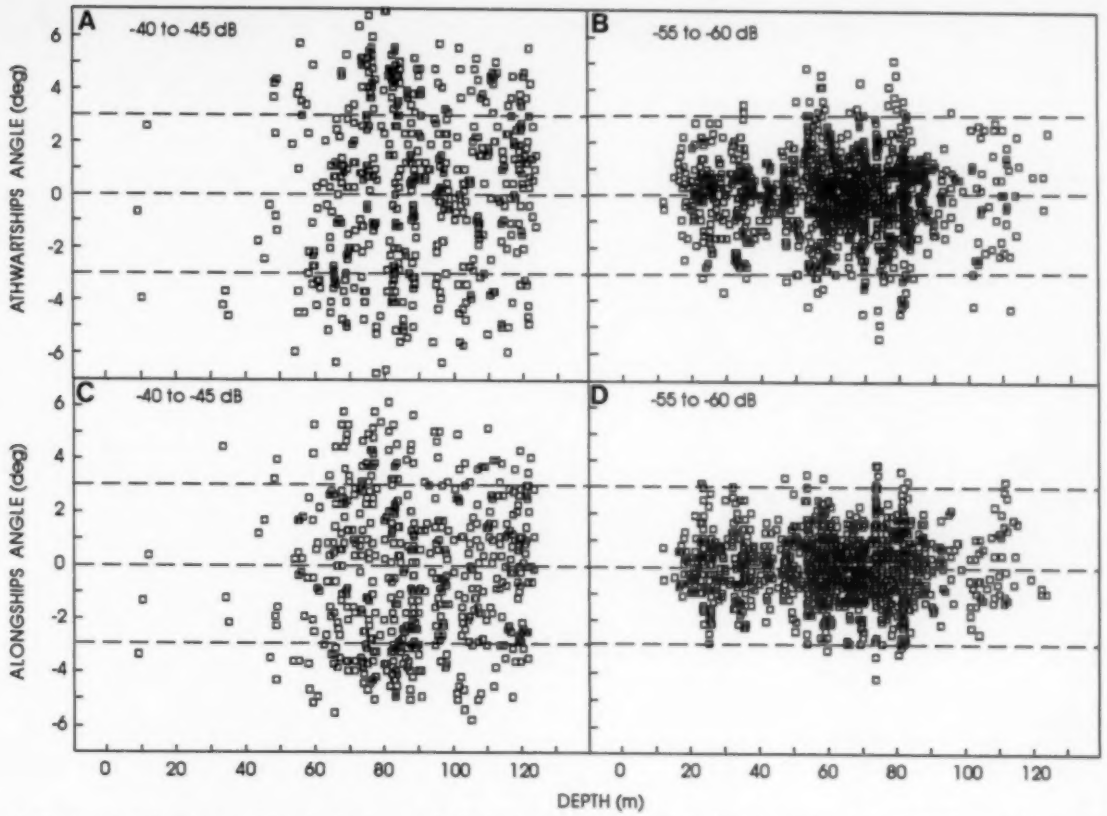

Fig. 2. Scatterplot showing position in the beam of all single targets isolated during the cruise. (A and B) Targets between −40 and −45 dB; (C and D) targets between −55 and −60 dB.

and (b) the sample-to-sample variation in bearing in both directions was less than 3 units (0.4°) for at least six successive samples. These conditions are similar to those imposed by Dengbol and Lewy (1990) and Brede et al. (1990) in isolating single fish echoes from ES400 data. We found them to be appropriate for recognizing single sphere echoes, both in a test tank and at sea.

In the processing phase, potential single fish echoes were screened further according to shape, being rejected if the envelope did not show a reasonably monotonic variation about a single peak. An example of an echo satisfying all the above criteria is given in Fig. 1. In this case the threshold was set at 40 bits.

For each accepted echo, the angular bearing was used to compensate the peak recorded amplitude according to the position of the target in the beam, enabling TS to be estimated directly. Data for the compensation were obtained by fitting the amplitude and bearing of sphere echoes in different parts of the beam (obtained during the calibration) to Ona's (1990b) empirical beam function expression for the same type of transducer. The resultant expression, which was used in compensating all accepted echoes in the experiment, was

$$(1)\quad B(\alpha,\beta) = 2^{-\left\{\left[(\alpha-\Delta\alpha)/0.5\alpha_1\right]^2+\left[(\beta-\Delta\beta)/0.5\beta_1\right]^2\right\}^{1.1}}$$

where α and β are the bearings in the alongships and athwartships directions, respectively, α_1 and β_1 the half-power beamwidth in these two directions, and $\Delta\alpha$ and $\Delta\beta$ the angular offsets in the phase detectors, measured during calibration.

For part of the study, a multichannel digital echo-integrator (Anonymous 1986) was also available and was used to estimate volume back-scattering strengths in 5-m channels throughout the water column. The integrator was coupled to the EK400 receiver and calibrated by sphere at the same time as the ES400.

Patterns in the distribution of target bearing with depth for different signal strengths were examined for evidence of bias arising from the application of a threshold (equivalent to an echo level of −66 dB) in the target-recognition software. Comparable results are presented in Fig. 2 for strong (−40 to −45 dB) and weak (−55 to −60 dB) targets. Strong targets were detected relatively evenly within the examined sector of the beam (7° on either side of the axis). In contrast, comparatively few weak targets were detected more than 3° off-axis, indicating a bias against weak targets on the edge of the beam. To minimize this effect, only targets located less than 3° off-axis were considered. Within this sector, no obvious patterns indicative of bias against weaker targets with increasing depth were evident, suggesting that the targets were equally detectable throughout the depth range considered.

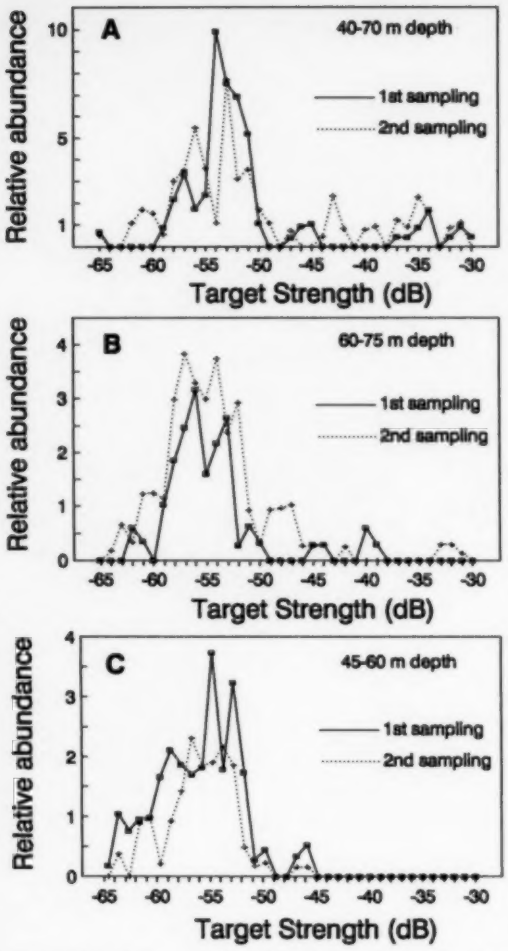

FIG. 3. Comparison between pairs of TS frequency distributions collected over similar transects. Time lapses between samples were (A) 90 min and (B and C) 24 h.

Finally, relative indices of abundance were calculated for each experiment according to the expression

$$(2)\quad I = \frac{k}{N}\sum_{i=1}^{n}\frac{1}{D_i^2}$$

where n is the number of targets fulfilling the selection criteria, N the number of pings transmitted in the experiment, D_i the depth of the ith target, and k a scaling factor. The depth factor is necessary to account for the increasing sampling volume with depth (e.g., Dengbol and Lewy 1990). The expression assumes that any bias in single target selection is independent of depth, i.e., that densities were sufficiently low for the probability of echo overlap to be negligible, even at maximum range. Echo-chart recordings support this assumption for juvenile hake, showing widely separated individual targets, even close to the bottom (e.g., see Fig. 8). Also, echo-integrator and TS data from the hake targets between 80 and 100 m depth (see Fig. 4C), which were exceptionally dense, suggest that even in this case, the probability of more than one fish occupying the pulse volume at that depth was less than 1%.

Results

To establish the consistency of the TS distributions obtained, paired experiments were carried out over similar areas at spaced time intervals. The objective was twofold: (a) to assess the consistency of the method in reflecting the fish population under study (i.e., if the same population is sampled repetitively the TS distributions should be similar) and (b) to examine the change in TS distributions associated with short-term temporal changes in community composition and behaviour.

The paired experiments (Fig. 3) were in good overall agreement with each other, suggesting that the TS distributions reflected the composition of each community accurately. In the first experimental example (Fig. 3A), targets were recorded between 40 and 70 m depth for approximately 5 min and then recorded again over the same depth range for a similar time period 90 min later. In the remaining examples (Fig. 3C and 3D), paired samplings were separated by 24 h. It is important to note that these pairs are not considered to be replicate samples from the same population because of small-scale temporal and spatial variability in the relative abundance of the dominant species in the community. Slight differences probably reflect changes in the dorsal aspect of fish (e.g., MacLennan and Simmonds 1992), or small differences in the size distribution of the targets insonified. Of a total of seven comparative experiments carried out in similar manner, only one resulted in a substantial difference between paired TS distributions.

Our next objective was to investigate whether monospecific, unimodal communities result in unimodal distributions of TS, which was motivated by observations of bimodalities in TS frequency distributions obtained from unimodal populations of walleye pollock (*Theragra chalcogramma*) (Traynor and Williamson 1983) and Pacific whiting (*Merluccius productus*) (Williamson and Traynor 1984). Data for all these experiments were obtained from a comparison between TS distributions and the length and species composition of midwater trawl catches made concurrently from the same depths. The results of two of these experiments are presented in Fig. 4, showing size and TS frequency distributions of largely monospecific populations of juvenile hake, one at 20–40 m depth (Fig. 4A and 4B) and the other between 80 and 100 m depth (Fig. 4C and 4D). Modes in total length of 14 and 15 cm corresponded to TS peaks at −51 and −48 dB, respectively. The weaker, less abundant targets in Fig. 4A perhaps originate from a population of small pelagic gobies (*Sufflogobius bibarbatus*) which were also present in the water column (Fig. 4B). A few stronger targets are evident in Fig. 4C, probably reflecting the horse mackerel (*Trachurus trachurus capensis*) (27–34 cm total length), which were also in the trawl collections, but less abundant than hake. Two more examples of near-monospecific catches are presented in Fig. 5. In the first illustration (Fig. 5A and 5B), a population of juvenile hake of 15-cm mode was associated with a TS peak centred at approximately −50 dB. Small gobies and larger horse mackerel were also present in the catches, contributing to the broader TS spectrum. The second example (Fig. 5C and 5D) shows the size distribution of ribbon fish (*Lepidopus caudatus*)

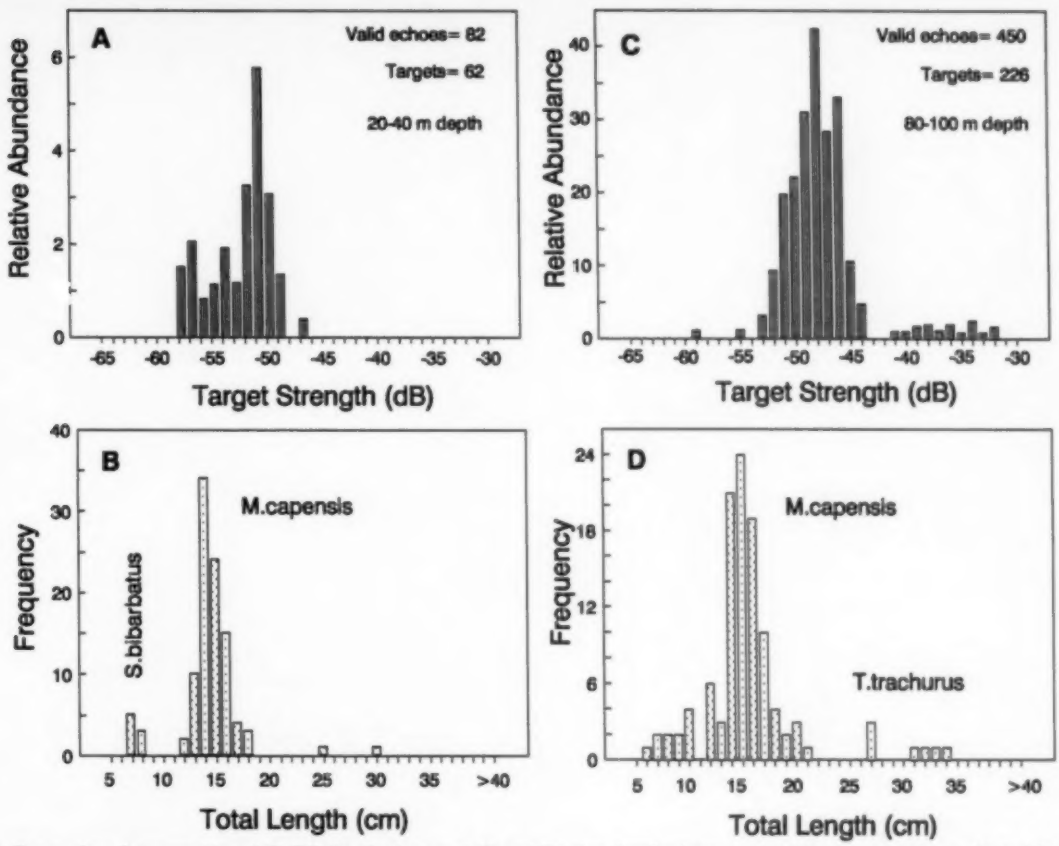

FIG. 4. Comparison between (A and C) TS distributions and (B and D) size distributions obtained from net catches collected from two deep monospecific communities of juvenile hake.

between 112 and 120 m depth, and the TS distribution for the fish population between these depths. In the four essentially unimodal populations displayed in Fig. 4 and 5, single peak modes in TS values were observed, which was the general trend in other monospecific populations of juvenile hake encountered during the study.

Two examples illustrating the acoustic discrimination of multispecific assemblages are presented in Fig. 6 and 7. The size frequencies were constructed from pooled midwater trawl collections, taken at four depth strata of the water column, which reflected the size distribution of the midwater community. TS distributions were obtained from depth strata similar to those sampled by the net and were combined taking into account the volume insonified at each depth. The first example (Fig. 6) shows a community of small gobies, juvenile hake, horse mackerel, and Cape gurnard (*Chelidonichthys capensis*). The last two species, which overlapped in size, gave a broad distribution of TS values greater than −42 dB. The modal length of the juvenile hake (15 cm) corresponded to a TS mode centred between −46 and −53 dB. This corresponds to a fivefold range in backscattering cross section, compared with about a twofold range in fish cross-sectional area and about a threefold range in their mass. The broader distributions of TS values compared with fish size are to be expected because of variation in aspect and the statistical nature of back-scattering intensities from individual fish (e.g., Clay and Heist 1984; Denbigh et al. 1991). In the next illustration (Fig. 7), even though horse mackerel and gurnard were less abundant than in the previous example, they were still identifiable in the TS distribution. A second peak in the TS distribution, centred at −47 dB, probably arose from a population of round herring (*Etrumeus whiteheadi*) of lengths ranging between 19 and 23 cm (Fig. 7). The main peak in the TS distribution arises from the large proportion of juvenile hake in the assemblage.

Figure 8 shows an echo-chart representing a multispecies fish community that is dominated by a dense layer of anchovy (*Engraulis capensis*) recruits in the upper 20–30 m, with single targets of larger fish, at lower densities, throughout the water column. TS values could be obtained from the dense layer of anchovies by the split-beam system, but the relative abundance index is negatively biased because only a few single echoes could be isolated from the layer. However, valid TS and relative abundance estimates were obtained for the larger, nonshoaling individuals and are presented in Fig. 9 as a three-dimensional structure. The figure was derived by producing TS distributions at 10-m depth intervals throughout the water column. The water column is dominated by a single peak at −49 dB in the upper 30 m,

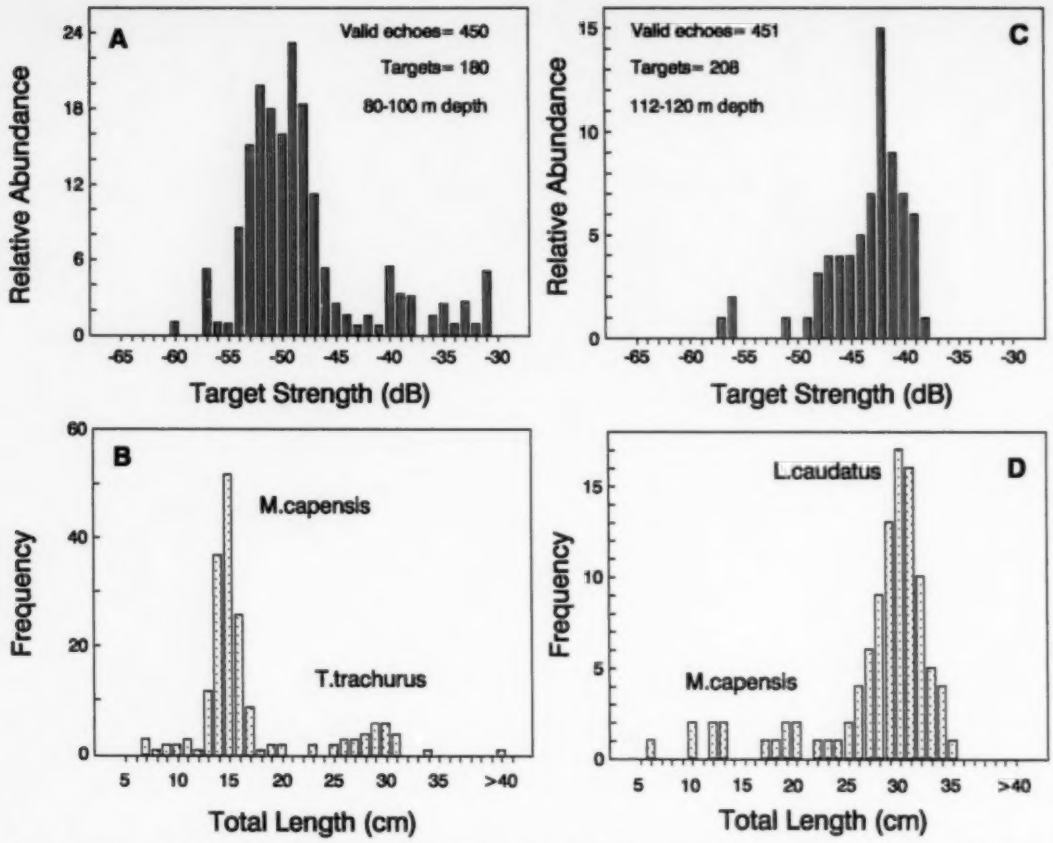

FIG. 5. Comparison between (A and C) TS distributions and (B and D) size distributions obtained from net catches collected from largely monospecific communities of (A and B) juvenile hake and (C and D) ribbon fish.

which is close to that of juvenile hake (peaks in Fig. 4–7). Abundances, however, decrease sharply with depth until 60 m, between which depth and the bottom targets of similar and higher strength than those near the surface were again abundant. Strong targets were recorded close to the seabed, suggesting that larger fish were present at that depth. The size distribution of the fish community was derived from midwater and bottom trawl catches and grouped into subsurface (0–40 m depth), midwater (50–80 m depth), and bottom trawls (Fig. 10). The subsurface catches were dominated by anchovy recruits of 5–10 cm, although their abundance could not be compared with the second peak of juvenile hake (10–17 cm), as the mesh was too coarse to retain the small anchovy efficiently. All other catches were dominated by young hake, larger individuals being less abundant in midwater than on the bottom. Horse mackerel, gurnard, and St Joseph sharks (*Callorhynchus capensis*) dominate the larger size class of fish, presumably accounting for the higher TS values close to the bottom in Fig. 9.

Discussion

The results presented suggest that the composition and abundance of certain low-density fish communities can be estimated by means of a split-beam echo-sounder. Considering the close agreement we obtained between the modes in the size and TS distributions, it seems that split-beam echo-sounders have the potential to resolve the vertical distribution of certain multispecies fish assemblages. Accordance between size and TS modes has been observed before, using both indirect (Robinson 1982; Halldórson and Reynisson 1983; Lindem 1983) and direct methods (Forbes 1985; MacLennan and Forbes 1987; Rudstam et al. 1987), but the use of TS analysis for studying community ecology has been hampered by large variation in TS and the difficulty in discriminating objectively among species of scatterer. The physiological condition of the animal, notably the state of the swim bladder, is a major source of variation in TS (Ona 1990a). Also, TS depends strongly on the orientation of the target relative to the acoustic beam, which in turn is dictated by the behaviour of fish (e.g., Nakken and Olsen 1977; Buerkle 1987; MacLennan et al. 1990). For example, Nakken and Olsen (1977) have shown that the maximum TS of cod at 38 kHz can change by up to 6 dB with a change in tilt angle of about 13°. It is therefore advisable to regard TS as a stochastic parameter and carefully assess the adequacy of the community under study to be resolved through TS methodology in terms of species diversity and fish abundance. Our results suggest that reliable target identification by aimed net trawling can greatly facilitate studies of fish communities through analysis of TS distributions.

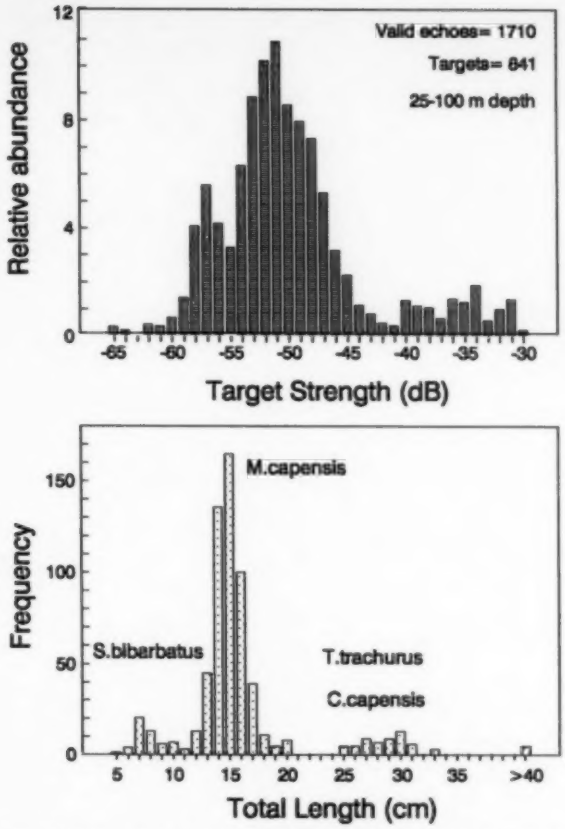

FIG. 6. Comparison between the TS distribution and size distribution derived from net catches of a multispecific community between 25 and 100 m depth.

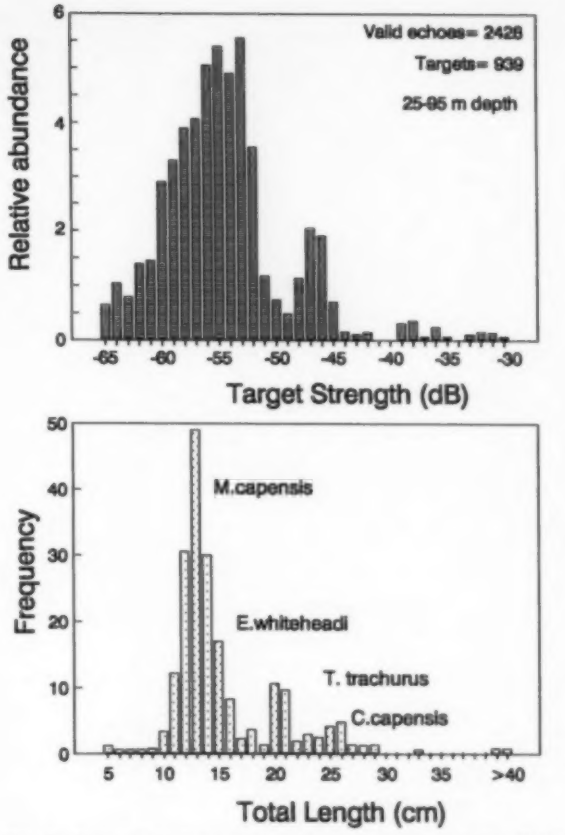

FIG. 7. Comparison between the TS distribution and size distribution derived from net catches of a multispecific community between 30 and 95 m depth.

The advantages of acoustic versus conventional net sampling are threefold: (a) it can achieve a much higher spatial and temporal resolution than net sampling, (b) it is free of the central problems associated with net sampling for community analysis (i.e., net avoidance and selectivity), and it offers a means of quantifying the migratory behaviour of some species from the bottom to midwater, particularly if coupled with echo-integration techniques. One limitation of the present TS analysis is the restriction concerning the degree of fish density to which it can be applied. The densities of the species analyzed here were generally low and comparable between species. With highly aggregated populations, however, the echoes could overlap to such an extent that very few single targets would be detected. There would also be doubt as to whether the TS values of isolated single fish were representative of the aggregated part of the population. We are currently developing new systems aimed at isolating single targets at higher densities than is possible with the system described here to alleviate these problems. A further limitation in the present data is that all acoustic data were obtained from populations that were more than 1–2 m above the seabed, therefore excluding populations that live in close contact with the bottom during the night. Results from over 100 bottom trawls taken around the clock at a fixed station during 11 cruises in the Benguela ecosystem suggest that approximately 20% of the *Merluccius capensis* biomass remains close to the bottom at night (Sea Fisheries Research Institute, unpublished data). Most of this biomass would not have been adequately sampled acoustically.

On the hake recruitment grounds studied here, there were very few other groundfish species, most of which remained close to the bottom during the night. Juvenile hake, however, made nocturnal vertical migrations towards the surface. Approximately 10% by number of the juvenile hake population illustrated in Fig. 9 (assumed to be those targets between −46 and −55 dB) were deeper than 80 m during the study, while 65% were shallower than 25 m. Nocturnal movement of juvenile hake towards the surface has been observed by Pillar and Barange (1993), who related this movement to foraging behaviour. The communities under study seem to be highly structured assemblages whose aggregating and migratory behaviour is likely to be dictated by physical mechanisms and/or biological interactions. Further progress in the identification and quantification of such structures would improve our present capacity to understand the functioning of the communities of which they form a part.

The actual TS values obtained for the different species are of interest. Table 1 summarizes the average TS and size for several species examined during experiments where tar-

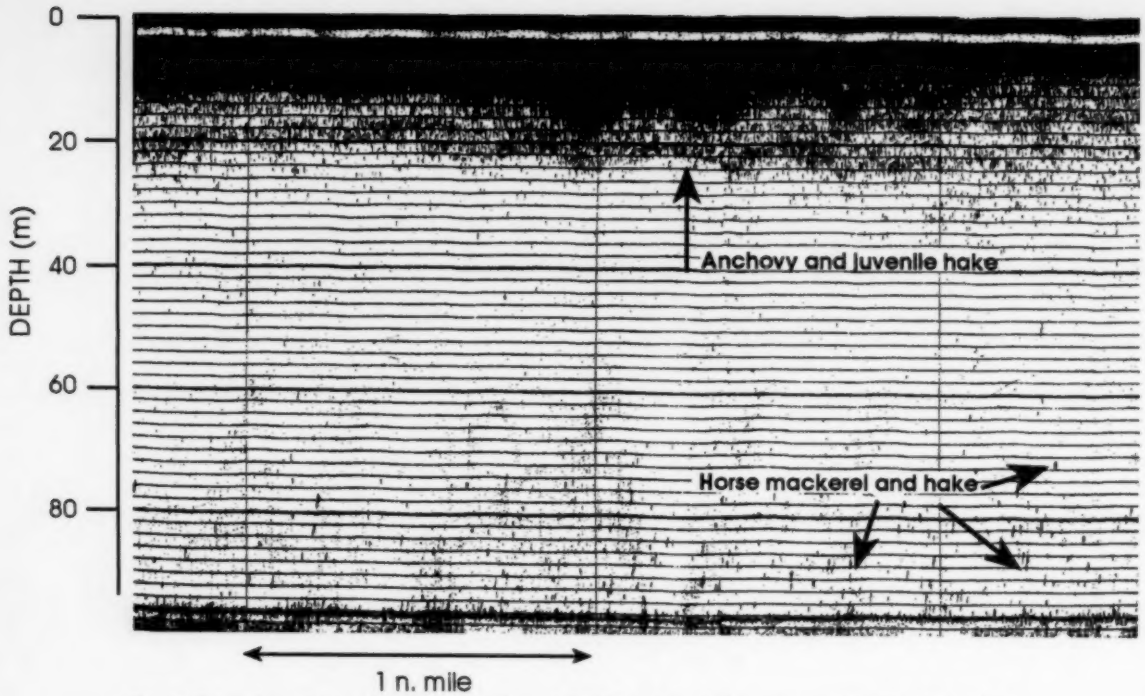

FIG. 8. Echo-chart obtained during collection of the TS and catch data presented in Fig. 9 and 10.

TABLE 1. Average size (total length) from net samples and average TS (derived from mean scattering cross sections) of *Merluccius capensis*, *Engraulis capensis*, *Etrumeus whiteheadi*, *Sufflogobius bibarbatus*, *Trachurus trachurus capensis*, and *Lepidopus caudatus* obtained during this study. Weight-normalized TS also presented.

Species	Total length (cm)	TS (dB)	Weight-normalized TS ($dB \cdot kg^{-1}$)
Merluccius capensis	11.86	−50.98	−32.07
	12.23	−53.34	−34.84
	13.95	−52.36	−35.62
	14.69	−49.03	−32.98
	14.69	−51.14	−35.09
	15.13	−49.65	−34.00
	15.16	−52.66	−37.04
	15.38	−49.34	−33.91
	15.60	−48.68	−33.44
Engraulis capensis	7.50	−57.84	−31.58
	7.34	−57.73	−31.16
Etrumeus whiteheadi	20.66	−46.61	−34.20
	20.71	−47.37	−34.99
Sufflogobius bibarbatus	9.42	−55.73	−36.89
	8.08	−56.88	−35.98
	6.50	−56.35	−32.53
Trachurus trachurus capensis	28.10	−39.52	−32.17
	27.50	−36.67	−29.04
Lepidopus caudatus	28.98	−42.44	—

get identification was considered to be reliable. Averages of mass-normalized TS, calculated according to the expression

$$(3)\quad \overline{TS}(dB \cdot kg^{-1}) = \overline{TS} + 10 \cdot \log_{10}(\overline{W})$$

where $\overline{W}$ is the average individual mass (kilograms), are presented to facilitate comparison between the species in our study and other published values for similar species elsewhere.

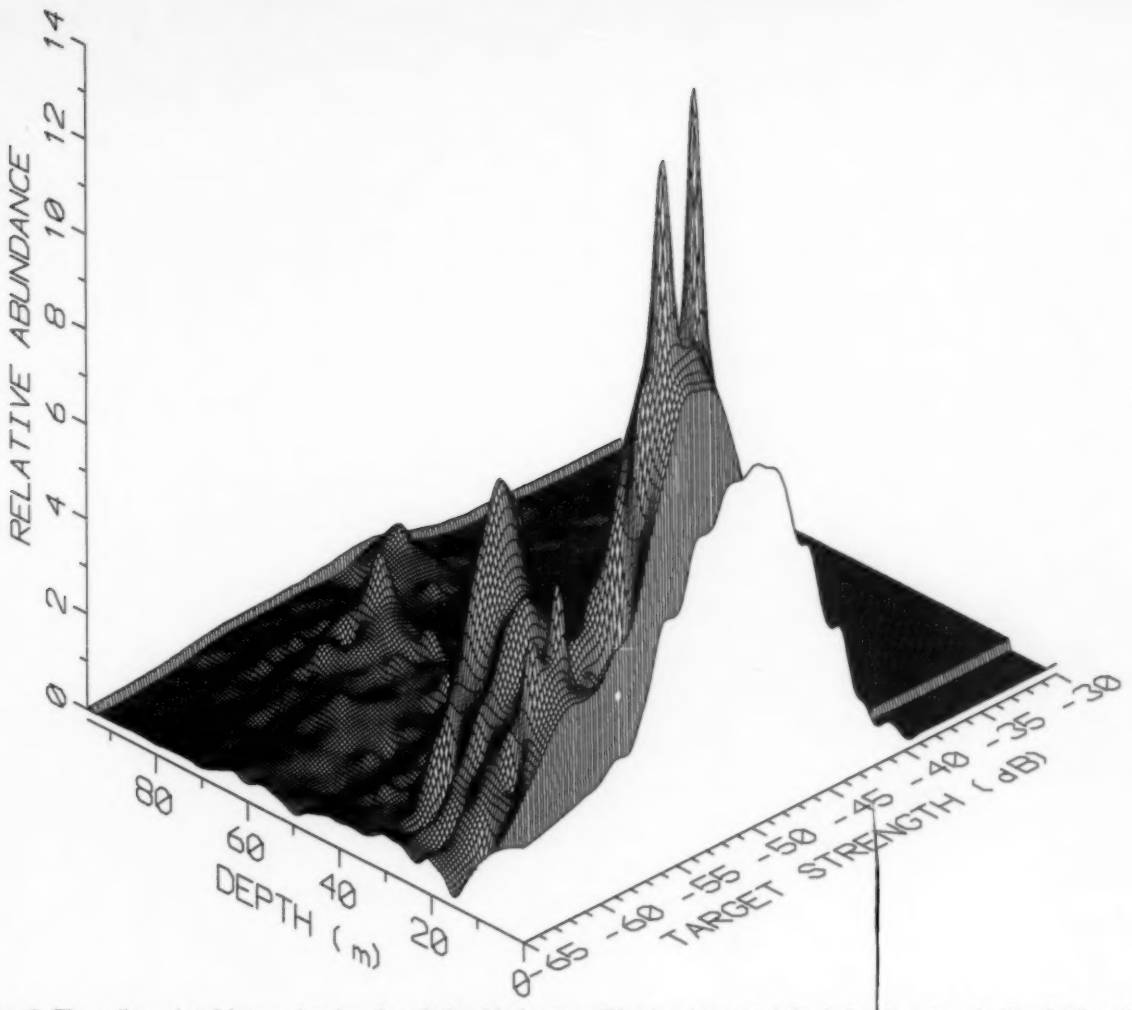

FIG. 9. Three-dimensional image showing the relationship between TS, abundance, and depth for the targets in Fig. 7. Note that no data were collected from the upper 10 m of the water column or within 3 m of the bottom (see text for explanation).

The round herring TS values agree closely with values expected from Foote's (1987) general clupeoid expression, which gives a value of −45.6 dB for a fish of 20.7 cm. Agreement is even closer with predictions from Halldórson and Reynisson's (1983) 38-kHz expression for Icelandic herring (*Clupea harengus*) which gives a value of −46.9 dB for a 20.7-cm fish. The anchovy values differ by about 3.4 dB from those predicted by Foote's clupeoid expression (−54.4 dB for a 7.5-cm fish) and by about 1.3 dB from those predicted by Halldórsson and Reynisson's expression for herring (−56.5 dB). We note, however, that since both expressions were derived from measurements on much larger fish (typically 20 cm), the discrepancies could be at least partially due to the extrapolation to smaller sizes. Average TS per unit of weight for *Merluccius capensis* varies between −32.7 and −37.0 dB·kg^{-1}, which agrees relatively well with values reported for the gadoids blue whiting (*Micromesistius poutassou*) (−33 to −33.5 dB·kg^{-1}, Robinson 1982) and Pacific whiting (−35 to −36 dB·kg^{-1}, Williamson and Traynor 1984), although it is lower than expected for other gadoids of similar size (−28.1 dB·kg^{-1} for a 15-cm fish, Foote 1987).

The only published values for horse mackerel TS at 38 kHz that we are aware of are a measurement by Nakken and Olsen (1977) on a single tethered 33-cm specimen (species not reported, but probably *Trachurus trachurus*) and several measurements of 32- to 39-cm specimens of *Trachurus murphyi* by Torres et al. (1984). The former reported a value of −34.0 dB and the latter measurements ranging between −35 and −37 dB, which are broadly consistent with our values for somewhat smaller specimens (Table 1). Our results for horse mackerel are also in general agreement with more comprehensive results obtained subsequently from a horse mackerel survey on the Cape south coast (−31.9 to −33.2 dB·kg^{-1}, Barange and Hampton 1993). We are not aware of any published TS values for any of the other species listed in Table 1.

There could be a number of explanations for the com-

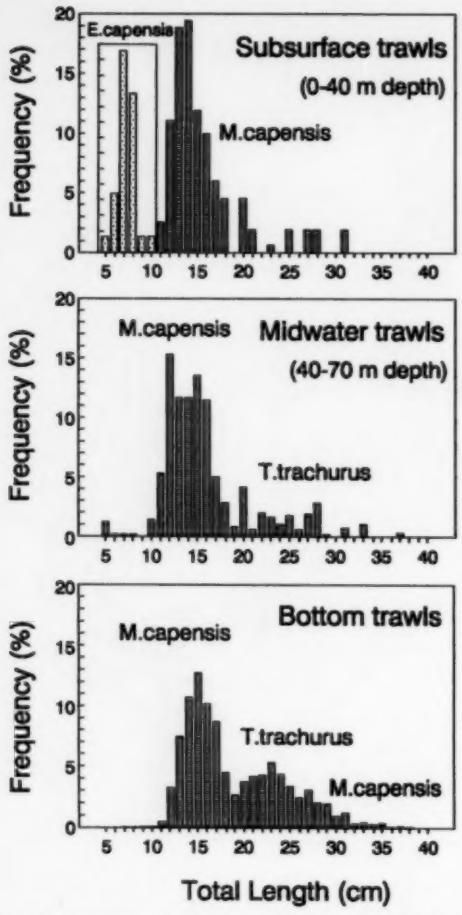

FIG. 10. Size frequency distributions obtained from trawling at several depth intervals during the collection of TS data presented in Fig. 9. Relative abundance of anchovy not comparable with the other species because of differences in catchability.

paratively low TS values recorded for the juvenile hake. Since hake are physoclists, the extensive vertical migrations that juveniles are known to perform (Pillar and Barange 1993) suggest that either they have a relatively small swim bladder or that it is severely compressed, e.g., by feeding. The latter possibility seems particularly real, as a large proportion of the juvenile hake caught off the bottom had full stomachs (Pillar and Barange 1993). We note that Ona (1990a) has found a reduction of up to 90% in swimbladder volume for cod with full stomachs, which would clearly result in a substantial reduction in TS. Careful studies on the relationship between TS, activity, and physiological state are needed. Fortunately, the suitability of juvenile hake for in situ TS studies makes such an investigation feasible.

We conclude that split-beam acoustic techniques can be used effectively to estimate the size structure, numerical abundance, and vertical distribution of low-density fish assemblages, offering a number of advantages over trawl net collections, not the least of which is the capacity for real-time examination of spatial variability.

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Relationships between Common Biological Reference Points Used as Thresholds and Targets of Fisheries Management Strategies

Pamela M. Mace

National Marine Fisheries Service, 1335 East-West Highway, Silver Spring, MD 20910, USA

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Relationships between various biological reference points (BRPs) used to define thresholds and targets of fisheries management strategies were examined for a range of combinations of life history characteristics. Rank orderings of the selected BRPs were strongly influenced by the degree of density dependence in the underlying spawning–recruitment (*S–R*) relationship. The validity of $F_{0.1}$, F_{max}, $F_{20\%}$ (the fishing mortality at which spawning per recruit is 20% of the maximum), and other reference fishing mortality rates as approximations to F_{msy} or as thresholds of overfishing is highly dependent on life history characteristics, particulary the degree of density dependence in the *S–R* relationship. It is recommended that $F_{40\%}$ be adopted as a target fishing mortality rate when the *S–R* relationship is unknown and that threshold levels of biomass be related to the estimated or assumed degree of density dependence in the *S–R* relationship. Two new methods of calculating threshold biomass levels are suggested as alternatives to the familiar 20% B_0 rule.

Nous avons examiné les relations entre divers points de référence biologique (PRB) servant à définir les seuils et les cibles des stratégies de gestion des pêches pour une gamme diverse de combinaisons de caractéristiques biologiques. Les ordres de classement des PRB choisis étaient fortement influencés par le degré de dépendance par rapport à la densité dans le rapport des géniteurs aux recrues posé au départ. La validité de $F_{0.1}$, F_{max}, $F_{20\%}$ (la mortalité par pêche à laquelle le rapport géniteurs-recrues est de 20 % du maximum) et d'autres taux de mortalité par pêche, servant de référence comme approximations de F_{rms} ou comme seuils de la surpêche, dépend fortement des caractéristiques du cycle biologique, et particulièrement du degré de dépendance par rapport à la densité dans le rapport géniteurs-recrues. Il est recommandé d'adopter comme taux cible de mortalité par pêche $F_{40\%}$ lorsqu'on ne connaît par le rapport géniteurs-recrues, et de mettre en rapport les niveaux seuils de la biomasse avec les degrés estimés ou supposés de dépendance par rapport à la densité dans le rapport géniteurs-recrues. Nous proposons deux nouvelles méthodes pour calculer les niveaux seuils de la biomasse, méthodes qui peuvent remplacer la règle familière de 20 % B_0.

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There are two general classes of risk or loss that need to be considered when formulating fisheries management strategies: the risk that yields will fall below the maximum attainable level and the risk that the stock will fall below some minimum size. To some extent, the first represents a risk to the fishery and the second a risk to the stock; however, if the stock "collapses", then it is likely that the fishery will also "collapse". Essentially, the former risk is the risk of not attaining a desirable target; the latter is the risk of falling below an undesirable threshold. The challenge for fisheries scientists and managers is to find a fishing strategy that achieves either both objectives or a compromise between the objectives. The usual approach has been to base fishing strategies on biological reference points (BRPs) such as target or threshold fishing mortality rates (F) and/or target or threshold biomass levels (B). These BRPs are often stated to be "conservative", "risky", or "near-optimal" but there are rarely sufficient data to make a sound judgement, and the same reference point may be categorized differently depending on the stock under consideration and the investigators' perceptions about the resilience of the stock.

The purpose of this paper is to evaluate the ability of selected BRPs to achieve long-term average yields approximating maximum sustainable yield (MSY) while at the same time avoiding overfishing thresholds associated with an unacceptable or undesirable stock condition. In part, this study is an extension of previous work by Deriso (1982, 1987), Beddington and Cooke (1983), Clark (1991), and others who have investigated the relationships between the true (deterministic) MSY and other BRPs. The main extensions here are the inclusion of a wider array of BRPs, a wider range of life history characteristics, and more explicit consideration of the ability of the reference points to achieve fishing targets while simultaneously avoiding overfishing thresholds. Thresholds and targets are expressed in terms of both F and B, and new methods for representing biomass thresholds are proposed.

The BRPs discussed include the constant fishing mortality rate that produces MSY (F_{msy}), the fishing mortality rate that equals the natural mortality rate ($F = M$), two reference fishing mortality rates from yield per recruit (YPR) analysis ($F_{0.1}$ and F_{max}), reference fishing mortality rates from spawning per recruit (SPR) analysis (e.g., $F_{20\%}$ and

$F_{35\%}$), the threshold fishing mortality rate associated with extinction of the stock (referred to here as F_τ), the equilibrium biomass levels corresponding to the first four of these reference fishing mortalities (B_{msy}, $B_{F=M}$, $B_{0.1}$, and B_{max}), and various percentages of B_{msy}, virgin biomass (B_0), and virgin recruitment (R_0). Although the analysis is based on deterministic models, it can also be used to guide the formulation of control laws in stochastic systems, e.g., the choice of an appropriate threshold in control laws that limit the frequency at which biomass is permitted to fall below the threshold. The analysis may also provide guidance on the selection of reference points in situations where essential information on life history characteristics is lacking.

Methods

The question of which BRPs are best in which situations is complex. To make the problem tractable, the following major simplifications were adopted: economic objectives were not considered explicitly, fishing strategies were formulated as constant F strategies, and results are presented in terms of deterministic equilibria. The target or goal of a fishing strategy is specified to be some constant F that will achieve a long-term average yield approximating MSY while at the same time staying "far away" from the ultimate threshold of F_τ (which has a corresponding equilibrium B of zero). The obvious candidate for this target is F_{msy}; however, F_{msy} cannot be estimated unless the spawning–recruitment (S–R) relationship is known, and for certain S–R relationships, it could be dangerously close to the threshold. The problem is to choose a measurable F that provides the best compromise between approximating F_{msy} and avoiding stock collapse for a range of plausible S–R relationships and other life history characteristics.

The procedure developed to address this problem used standard age-structured population models with some parameters fixed and others varied between runs. Beginning-of-year numbers at age were calculated from

$$(1) \qquad N_{t+1} = N_t e^{-(F+M)}$$

where N = numbers, t = age, M = rate of natural mortality (0.1, 0.2, or 0.3), and F = rate of fishing mortality.

Annual growth was represented by the von Bertalanffy equation:

$$(2) \qquad W_t = W_\infty (1 - e^{-K(t-t_0)})^b$$

with

$$W_\infty = a' L_\infty^{b'}$$

where W = weight, L = length, W_∞ = asymptotic weight, L_∞ = asymptotic length (fixed at 50 cm), K = Brody growth coefficient (0.1, 0.2, or 0.3), t_0 = growth intercept (fixed at 0), and a' and b' = parameters (fixed at $a' = 0.01$, $b' = 3$).

Catch numbers at age, C_t, were calculated from the catch equation

$$(3) \qquad C_t = \frac{F}{F+M}(1 - e^{-(F+M)}) N_t.$$

Partial recruitment and maturity were both assumed to be knife-edged (0 below a given age and 100% above) with the age of recruitment, t_r, always equal to the age of maturity, t_m (3, 5, or 7). Spawning biomass was represented by the average mature biomass present during the year, calculated by multiplying equations (1) and (2), summing over mature ages, and multiplying the result by $(1 - e^{-(F+M)})/(F+M)$. Similarly, the yield in weight was calculated by multiplying equation (3) by equation (2) and then summing over ages.

For the main series of runs, recruitment was modelled using a Beverton–Holt S–R relationship (Beverton and Holt 1957):

$$(4) \qquad R = \frac{S}{\alpha + \beta S}$$

where R = recruitment in numbers, S = spawning biomass, and α and β = parameters with $1/\alpha$ = slope at the origin and $1/\beta$ = asymptotic recruitment (fixed at 10^8 recruits). Since the recruitment and maturity schedules coincided, the average recruited biomass and spawning biomass were identical, as were the (recruited) biomass per recruit (BPR) and the spawning biomass per recruit (SPR). The latter two quantities were obtained from the equation

$$(5) \qquad \mathrm{BPR} = \mathrm{SPR} = \left(\frac{1 - e^{-(F+M)}}{F+M}\right) \sum_{t=t_r}^{\infty} (N_t \, e^{-(F+M)(t-t_r)} W_t)$$

with

$$N_t = 1 \text{ at } t = t_r \; (= t_m).$$

Virgin recruitment (R_0) and virgin biomass (B_0 or S_0) were defined by the intersection of the S–R curve with the line through the origin having slope equal to the inverse of the spawning biomass per recruit at $F = 0$ ($\mathrm{SPR}_{F=0}$). Thus,

$$(6) \qquad B_0 = S_0 = \mathrm{SPR}_{F=0} \cdot R_0.$$

The extinction parameter, τ, was defined as the ratio between the slope (or equivalently the survival ratio, R/S) corresponding to $\mathrm{SPR}_{F=0}$ (i.e., $1/\mathrm{SPR}_{F=0}$) and the slope at the origin (i.e., $1/\alpha$). Therefore, τ is equivalent to

$$(7) \qquad \frac{\mathrm{SPR}_\tau}{\mathrm{SPR}_{F=0}}$$

where SPR_τ = threshold level of SPR (corresponding to the slope at the origin) and $\mathrm{SPR}_{F=0}$ = maximum possible SPR (corresponding to zero fishing). The product 100τ is also referred to as the "threshold %SPR" (e.g., Mace and Sissenwine 1993). F_τ is the corresponding fishing mortality rate. It follows that the parameter α in equation (4) is related to τ by

$$(8) \qquad \alpha = \mathrm{SPR}_{F=0} \cdot \tau.$$

Solving equation (4) at (B_0, R_0) using substitutions based on equations (6) and (8) results in two alternative expressions for R_0:

$$(9) \qquad R_0 = \frac{\mathrm{SPR}_{F=0} - \alpha}{\beta \cdot \mathrm{SPR}_{F=0}} \quad \text{or} \quad R_0 = \frac{1}{\beta}(1 - \tau).$$

$F_{0.1}$ and F_{max} were derived from YPR analysis (equation (A1) in Appendix A) by the standard method. $F_{20\%}$ and $F_{35\%}$ were defined as the fishing mortality rates corresponding to 20 and 35%, respectively, of $\mathrm{SPR}_{F=0}$ from SPR analysis. The equilibrium recruitment at these and any other reference levels of F is given by

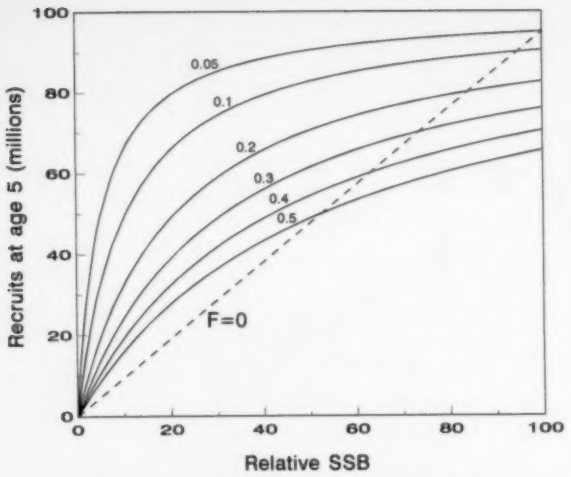

FIG. 1. Effects of τ on the shape of the Beverton–Holt *S–R* relationship (numbers above the curves are the values of τ). The broken line is the line with slope $1/\mathrm{SPR}_{F=0}$; the intersection of this line with the *S–R* curves defines the location of (B_0,R_0), or equivalently (S_0,R_0), and therefore represents the upper limit of the range of the *S–R* curves.

$$R_{F_{\mathrm{ref}}} = \frac{\mathrm{SPR}_{F_{\mathrm{ref}}} - \alpha}{\beta \cdot \mathrm{SPR}_{F_{\mathrm{ref}}}}$$

(10)

$$\text{or } R_{F_{\mathrm{ref}}} = \frac{1}{\beta}\left(1 - \tau \cdot \frac{\mathrm{SPR}_{F=0}}{\mathrm{SPR}_{F_{\mathrm{ref}}}}\right).$$

Corresponding levels of equilibrium yield and equilibrium biomass are given by the products

(11) $Y^*_{F_{\mathrm{ref}}} = \mathrm{YPR}_{F_{\mathrm{ref}}} \cdot R_{F_{\mathrm{ref}}}$

and

(12) $\mathrm{B}^*_{F_{\mathrm{ref}}} = \mathrm{BPR}_{F_{\mathrm{ref}}} \cdot R_{F_{\mathrm{ref}}}$.

F_{msy} is obtained as the value of $F = F'$ that maximizes the expression

(13) $X = F' \cdot (\mathrm{BPR}_{F'} - \alpha)$.

The corresponding MSY is

(14) $$\mathrm{MSY} = \frac{X}{\beta}.$$

Finally, the extinction threshold, F_τ, is obtained by finding the value of $F = F^*$ that satisfies the equation

(15) $\mathrm{SPR}_{F^*} = \alpha$.

In another series of runs, the Ricker *S–R* model (Ricker 1954) was used in place of the Beverton–Holt model. The Ricker *S–R* relationship is given by

(16) $R = aSe^{-bS}$

where a and b = parameters with a = slope at the origin and $b = (ae^{-1}/R_{\max})$, where $R_{\max}$ is the maximum recruitment (fixed at 10^8 recruits). For a given level of τ defining the slope at the origin, the extinction threshold fishing mortality rate (F_τ) is the same for both *S–R* models, but F_{msy} will differ. For the Ricker model, F_{msy} is the fishing mortality rate, F', that maximizes

(17) $X = F' \cdot \log_e(a \cdot \mathrm{SPR}_{F'})$.

Use of the Ricker model also required modification of equations (8), (9), and (10).

Based on previous studies, it was judged that the population parameters with the highest sensitivity were likely to be M, K, and τ. In the first series of runs, reference levels of F and B were calculated for all combinations of M = 0.1, 0.2, or 0.3; K = 0.1, 0.2, or 0.3; and τ = 0.05–0.5 in increments of 0.05, with all other parameters held constant. In the second series, the effects of changing the ages of recruitment and maturity were examined for the case $M = K = 0.2$ and τ = 0.05–0.5. For the third and final series, the Ricker *S–R* model was used in place of the Beverton–Holt model for the cases $M = K$ = 0.1, 0.2, or 0.3 and τ = 0.05–0.5. All equilibrium biomass levels were expressed in terms of $\%B_0$ (here equivalent to $\%S_0$).

The range of values selected for τ was based on the studies of Mace (1991) and Mace and Sissenwine (1993) where the median through the origin of observed *S–R* data was used as an estimate of the slope at the origin (i.e., the limit of the survival ratio as S approaches 0) and therefore the extinction thresholds denoted by SPR_τ and F_τ. The extremes of τ used here are close to the extremes estimated in these two studies. The upper limit of τ = 0.5 implies extremely low compensation (survival at low stock sizes only about twice that at the virgin size), while τ = 0.05 implies high compensation (survival at low biomass about 20 times the virgin rate). A default threshold of τ = 0.2 (survival at least five times the virgin rate) is commonly assumed (e.g., in overfishing definitions in fisheries management plans in the United States).

Results

Main Runs with Beverton–Holt S–R Model

When spawning stock biomass (SSB) was expressed in relative terms (e.g., as $\%B_0$ or $\%S_0$), the shape of the Beverton–Holt relationship was independent of both M and K, i.e., M and K only affected the scale on the SSB axis, not the absolute amount of recruitment. In contrast, the shape of the relationship was strongly influenced by τ (Fig. 1). For τ = 0.5, the relationship is almost linear through the origin over its entire range, while for τ = 0.05, recruitment is almost constant down to a level of about 20% B_0.

F_{msy} and F_τ both decrease with increasing τ and increase with K and M (Fig. 2). Both reference fishing mortalities have the highest sensitivity to τ, next to M, and last to K. For low values of τ (about 0.05–0.1), the extinction threshold fishing mortality rate, F_τ, was usually high, sometimes exceeding F = 3. F_{msy} was usually well below F_τ, ranging from 16.4% F_τ to about 43% F_τ over all parameter combinations. $F_{0.1}$, $F_{\max}$, $F_{20\%}$, and $F_{35\%}$ are not influenced by τ, but all increase with both M and K. For each M–K combination, $F_{0.1}$, $F_{35\%}$, and $F = M$ were of similar magnitude, with $F_{35\%}$ usually slightly higher than $F_{0.1}$, and $F_{0.1}$ slightly lower than $F = M$ for K = 0.1, almost identical for K = 0.2, and slightly higher for K = 0.3. $F_{\max}$ was only defined for four of the nine M–K combinations and was usually near the $F_{20\%}$ level.

Points of intersection with F_τ indicate parameter combinations where reference levels of F cease to be sustainable (in the deterministic sense). For $F_{\max}$ to be sustainable,

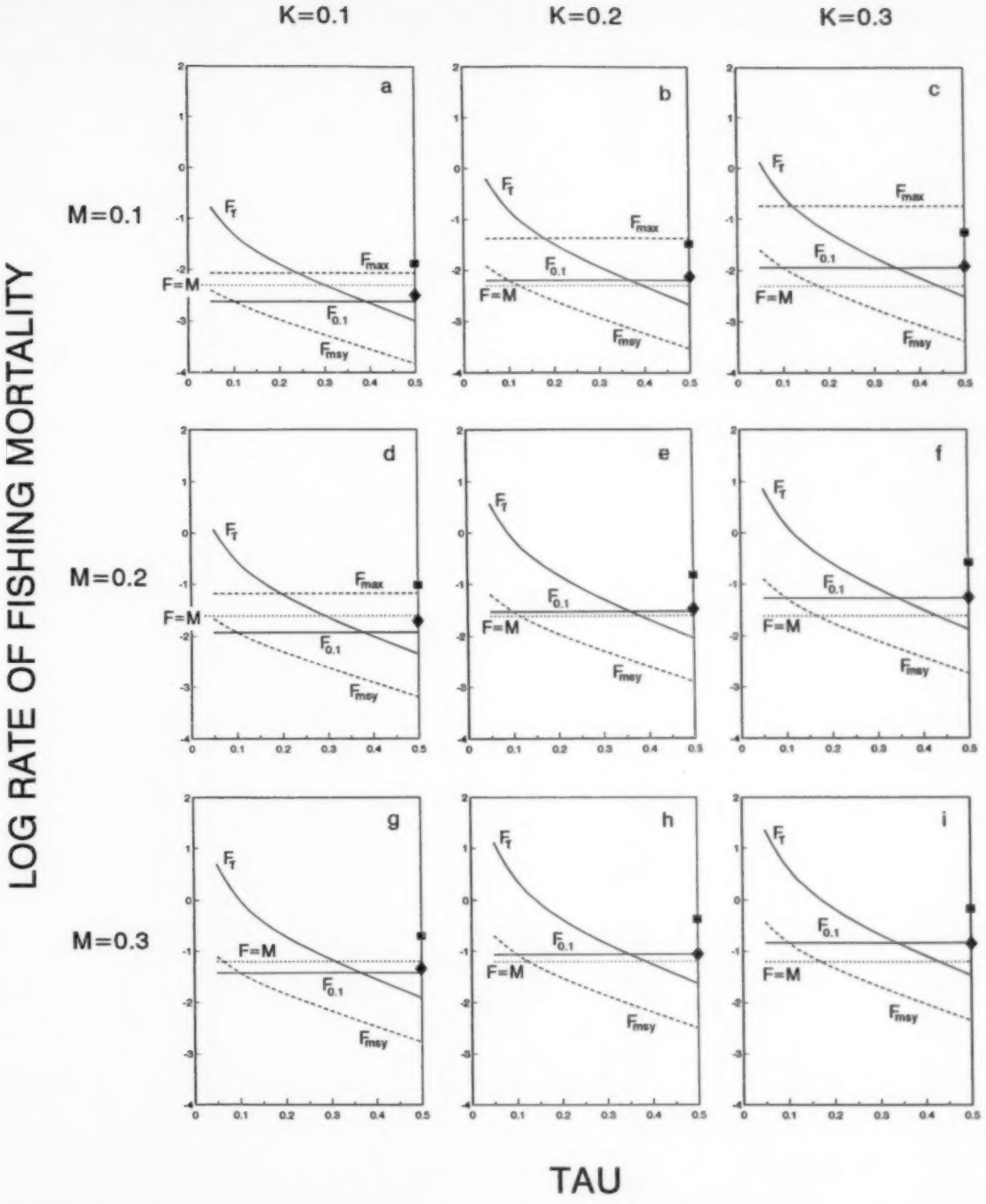

FIG. 2. Effects of various combinations of M, K, and τ on estimates of reference levels of fishing mortality (F) for the Beverton–Holt model: F_τ (solid curve), F_{msy} (broken curve), $F{=}M$ (dotted line), $F_{0.1}$ (solid straight line), F_{max} (broken straight line), and $F_{20\%}$ and $F_{35\%}$ (represented respectively by squares and diamonds on the right-hand side of the graphs). Fishing mortality was plotted on a log scale to make the figures readable.

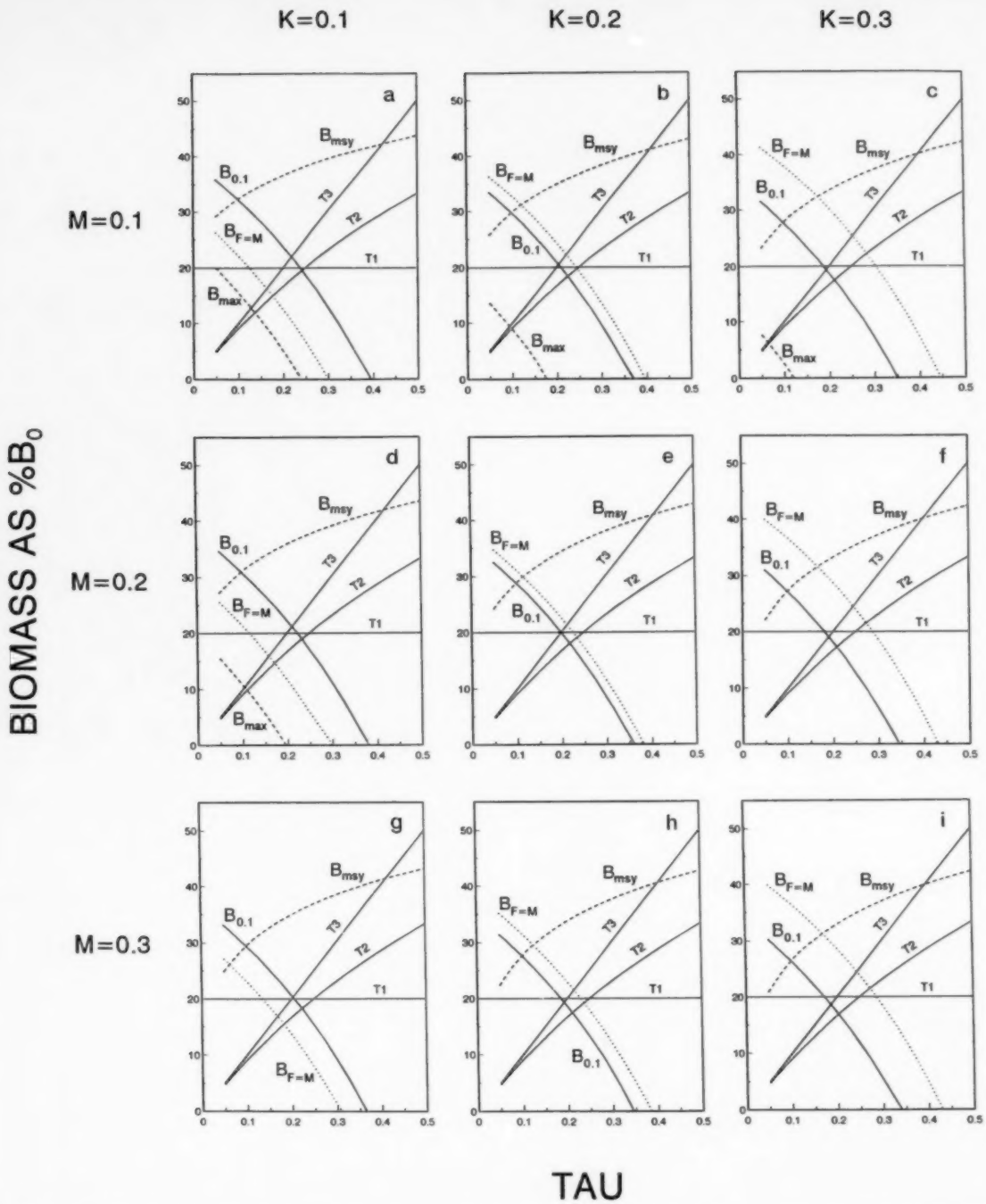

FIG. 3. Effects of various combinations of M, K, and τ on estimates of equilibrium levels of biomass (B) expressed as $\%B_0$ (or $\%S_0$) for the Beverton–Holt S–R model. Estimates of B_{msy} (heavy broken line), $B_{F=M}$ (dotted line), $B_{0.1}$ (light solid line), and B_{max} (light broken line) are the equilibrium biomass levels attained with the corresponding reference fishing mortality rates in Fig. 2. T1 represents the common threshold level of 20% B_0; T2 is the $\%B_0$ attained at 50% R_{max}; T3 is the line given by $\%B_0=100\tau$.

τ must be less than 0.15–0.25 depending on the parameter combination considered (Fig. 2). $F_{0.1}$ is sustainable for all parameter combinations with τ less than about 0.4. $F = M$ is sustainable for values of τ up to about 0.3, 0.38, and 0.43 for $K = 0.1$, 0.2, and 0.3, respectively.

F_{max} exceeded F_{msy} for all parameter combinations, as is always the case for the Beverton–Holt S–R relationship. $F_{0.1}$ was identical to F_{msy} at $\tau = 0.1$, less than F_{msy} for $\tau < 0.1$, and greater than F_{msy} for $\tau > 0.1$. This result held over all parameter combinations and is true in general whenever recruitment and maturity schedules coincide and the S–R relationship is given by the Beverton–Holt model (see Appendix A). $F = M$ was greater than F_{msy} for τ exceeding about 0.05–0.16, depending on K.

B_{msy}, the equilibrium biomass corresponding to F_{msy}, increases monotonically with τ when expressed as a percentage of B_0 (Fig. 3), although it is dome shaped when expressed in absolute terms because B_0 itself decreases with τ. B_{msy} was never less than the commonly used threshold of 20% B_0 (e.g., Beddington and Cooke 1983), but it approached this level (T1 in Fig. 3) for certain parameter combinations (e.g., $M = K = 0.3$ and $\tau = 0.05$ where B_{msy} was 20.9% B_0). It is interesting to note that the magnitude of $B_{0.1}/B_0$ was influenced relatively little by M or K, always intersecting 20% B_0 near $\tau = 0.20$ (range 0.18–0.24). In contrast, the point where $B_{F=M}$ fell below 20% B_0 ranged between about $\tau = 0.12$–0.30, depending on the M–K combination. B_{max} was almost always less than 20% B_0.

Effects of Age of Recruitment

A (simultaneous) change in the age of recruitment (t_r) and the age of maturity (t_m) alters the percentage of growth achieved at the age of recruitment (Table 1). Increasing t_r ($=t_m$) resulted in increases in $F_{0.1}$ relative to $F = M$, increases in the range of τ values over which $F = M$ was sustainable, increases in the level of τ at which $F_{msy} = M$, decreases in the equilibrium level of B_{msy} as a fraction of B_0, and decreases in the range of τ values over which $B_{F=M}$ fell below 20% B_0 (Fig. 4). However, over the 4-yr range of ages tested, none of the differences were pronounced.

Extension to Ricker

F_{msy} is the only reference F level that differs between the Beverton–Holt and Ricker models. For the parameter combinations considered in Fig. 2, F_{msy} estimates based on the Ricker S–R function were invariably higher than those derived from the Beverton–Holt S–R function, being at least twice as high for $\tau = 0.05$ and converging to a difference of at least 10% at $\tau = 0.5$. The reason for the difference is that for the same maximum R and slope at the origin (relative to the $F = 0$ replacement line), the excess of recruitment over the replacement level required in the absence of fishing is usually greater for the Ricker function, except at the extremes of spawning biomass (Fig. 1 and 5). The difference is particularly pronounced at low values of τ. In fact, for parameter combinations where F_{max} was defined, Ricker S–R estimates of F_{msy} usually exceeded F_{max} at $\tau = 0.05$, although they were always less than F_{max} for $\tau = 0.1$ or more (Fig. 6). Similarily, the level of τ at which F_{msy} intersected $F_{0.1}$ was higher for the Ricker model (occurring within a remarkably small range of τ of about 0.17–0.19 over the full set of parameter combinations), compared with the Beverton–Holt model (consistently, $\tau = 0.1$).

TABLE 1. Percentage of growth in length ($\%L_t/L_\infty$) and weight ($\%W_t/W_\infty$) achieved at the age of recruitment for the combinations of the Brody growth coefficient (K in equation (2)) and age of recruitment (t_r in equation (5)) considered in Fig. 2–4 and 6.

	$\%L_t/L_\infty$	$\%W_t/W_\infty$
$K = 0.1$		
$t_r = 5$	39.4	6.1
$K = 0.2$		
$t_r = 3$	45.1	9.2
$t_r = 5$	63.2	25.3
$t_r = 7$	75.3	42.8
$K = 0.3$		
$t_r = 5$	77.7	46.9

In comparison with the Beverton–Holt results (Fig. 3), the ratio B_{msy}/B_0 from the Ricker model was less sensitive to τ, but all other biomass ratios were considerably more sensitive to τ, ranging from as much as 70% B_0 at $\tau = 0.05$ to zero at $\tau = 0.25$–0.45 (Fig. 6).

Threshold Levels of Biomass

One problem with using a fixed $\%B_0$ (e.g., 20% B_0) as a threshold is that as compensation decreases (τ increases) and/or the age of recruitment is reduced, F_τ and F_{msy} both decline dramatically and any fixed F has a decreasing chance of being sustainable (Fig. 2, 4, and 6). It seems more logical to use a biomass threshold that increases as resilience decreases. One approach that takes account of the degree of compensation (i.e., the slope of the S–R relationship near the origin) is to express the threshold as a fixed percentage of the maximum recruitment (R_{max}). The S–R relationship can then be used to translate this into the corresponding $\%B_0$ (see Apprendix B). Threshold values of $\%B_0$ based on an arbitrary theshold recruitment level of 50% R_{max} (labelled T2) have been superimposed on Fig. 3, 4, and 6. Thresholds based on the Ricker S–R model (Fig. 6) differed only slightly from those based on the Beverton–Holt model (Fig. 3 and 4). For both models, T2 decreases in the same direction as τ but is independent of M and K. The relationship to B_{msy} is similar for all M–K parameter combinations: it approximates 50% B_{msy} for τ in the range of about 0.2–0.25 for the Beverton–Holt model and τ in the range of about 0.3–0.4 for the Ricker model and is less than 50% B_{msy} for smaller values of τ and greater than 50% B_{msy} for larger values. $B_{F=M}$ is generally below the suggested threshold for τ greater than about 0.3 and above the threshold for $\tau < 0.2$.

A simpler alternative solution to the problem of specifying a threshold level of $\%B_0$ that is less dependent on the exact form of the underlying S–R relationship is to set it at the same value as τ expressed as a percentage (i.e., $\%B_0 = 100\tau$; T3 in Fig. 3, 4, and 6). This is equivalent to equating threshold levels of $\%B_0$ with threshold levels of %SPR (equation(7)), although it is not strictly valid to use the two interchangeably (Appendix B). Equating the two results in a threshold biomass that is similar to that associated with 50% R_{max} (T2) at low τ, but much higher at high τ (Appendix B; Fig. 3, 4, and 6). However, T3 may be a reasonable threshold in cases where the form of the S–R

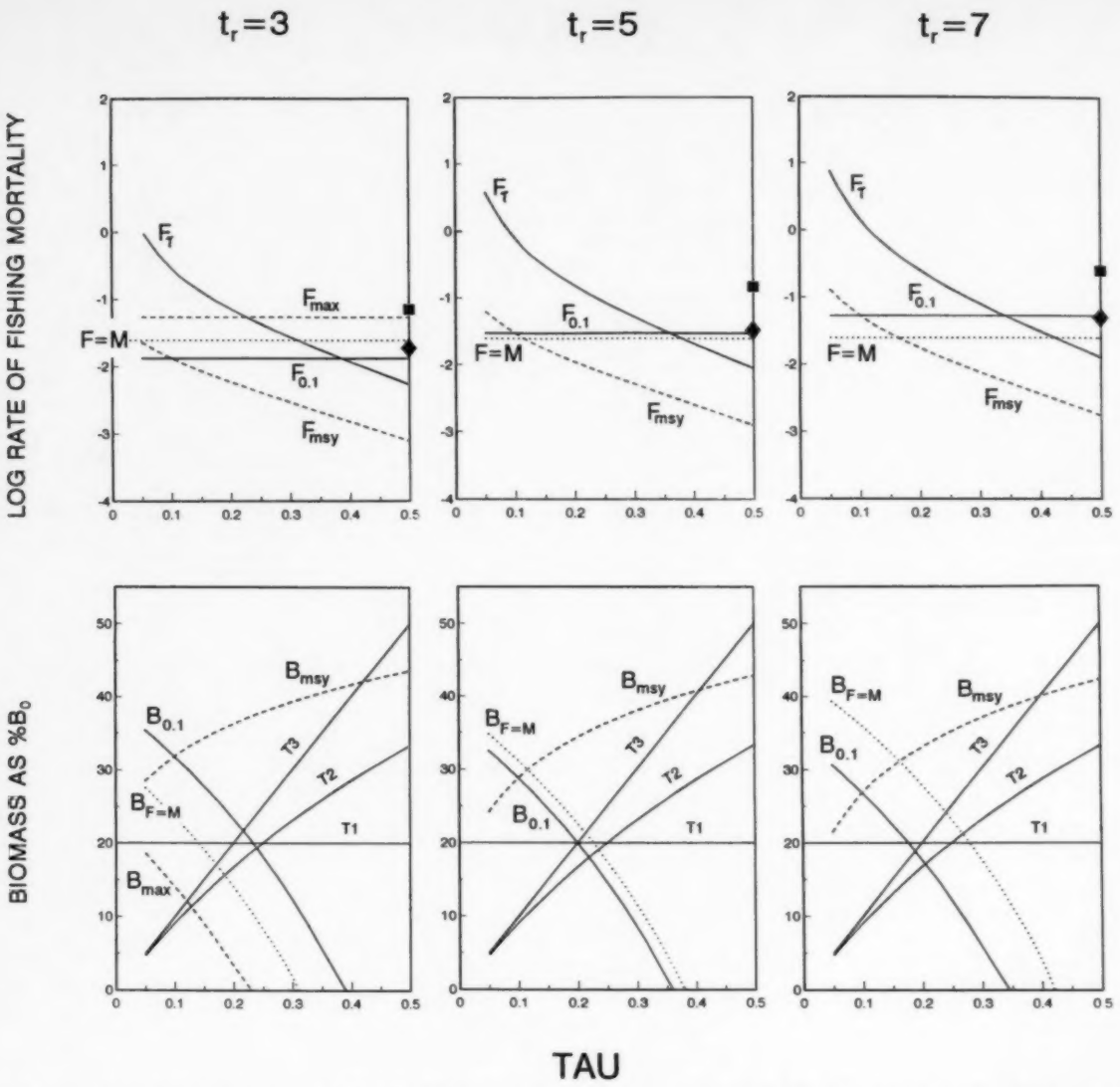

FIG. 4. Effects of the age of recruitment ($t_r = 3$, 5, or 7) on estimates of reference levels of fishing mortality (F) and equilibrium levels of biomass (B) expressed as $\%B_0$ for the Beverton–Holt model. See legends to Fig. 2 and 3 for details.

relationship is unknown. Like T2, it has the property of increasing with τ and represents a situation where recruitment is likely to have fallen appreciably relative to virgin or maximum levels. T2 is equivalent to 20% B_0 at $\tau = 0.25$ for the Beverton– Holt relationship and τ about 0.3 for the Ricker relationship; T3 is equivalent to 20% B_0 at $\tau = 0.2$.

Discussion

Which Values of τ Seem Credible?

Conclusions about whether particular BRPs are "conservative" or "risky" are highly dependent on the magnitude of τ (and, to a lesser extent, on other life history characteristics). To date, there have been few studies that can be used as a basis for selecting or rejecting particular values or ranges of τ. Even when *S–R* data are available, estimation of τ is hindered by (i) measurement errors, (ii) recruitment variability, (iii) lack of adequate contrast in *S*, and (iv) uncertainty about the form of the *S–R* relationship as a result of (i), (ii), and (iii). Shepherd (1982) proposed using the 90th percentile survival ratio of the *S–R* data points to estimate the slope of the *S–R* function at the origin; however, Sissenwine and Shepherd (1987) pointed out that *S–R* data points in the upper 10th percentile may just reflect anomalously favorable environmental conditions, not the ability to the population to sustain fishing under average environmental conditions. The latter authors proposed using the average or median observed survival ratio (*R/S*) as a safer estimate of the maximum survival ratio. In fact, the average or median

survival ratio is likely to be a biased estimator of the maximum survival ratio unless the *S–R* observations are restricted to low stock sizes where the *S–R* relationship can be approximated by a straight line through the origin. Otherwise, it will be conservatively biased for *S–R* observations that exhibit concavity (compensation) and liberally biased for *S–R* observations that are convex (depensation).

Mace (1991) and Mace and Sissenwine (1993) calculated median survival ratios for 83 sets of *S–R* observations taken from exploited fish stocks. Of these, 56% exhibited no significant departure from linearity through the origin, 44% exhibited significant concavity, and none exhibited significant convexity. However, the average value of τ (the inverse of the median survival ratio divided by $SPR_{F=0}$, i.e., their threshold %SPR expressed as a proportion) was almost identical for cases with and without concavity, so the two groups were not treated separately. The overall average value of τ was 0.19, and the 80th percentile of the results was approximately 0.3. Estimates for highly resilient species such as Atlantic cod (*Gadus morhua*) were frequently in the range τ = 0.05–0.15. Mace and Sissenwine (1993) recommended the observed average (rounded to 0.2) as a default overfishing theshold for stocks believed to have at least average resilience, but with insufficient *S–R* observations to estimate τ explicitly, and the 80th percentile result (τ = 0.3) for little-known stocks.

Clark (1991) rejected τ = 0.5 as too high for any fish stock (the parameter *A*, adopted by Clark from Kimura's (1988) reparameterization of the Beverton–Holt *S–R* relationship, is related to τ by the expression $\tau = 1 - A$) because the stock would be driven to extinction by a fishing mortality rate less than *M*. For the model and parameter combinations considered here, the highest τ at which $F = M$ was sustainable ranged from about 0.3 to 0.43 (Fig. 2, 4, and 6). The validity of using the criterion of sustainability of $F = M$ to set an upper bound on τ is debatable, but most fish stocks that have sustained fisheries for long periods have also sustained fishing mortality rates at least equal to *M*.

Choice of a lower bound is even more difficult. Clark (1991) used τ = 0.06 as the lower bound, rejecting the alternative of τ = 0.03 as too low for the majority of stocks because there would be "hardly any ill effect" of fishing at F = 1.0. However, 10-yr average fishing mortality rates exceeded F = 1.0 in 11% of the cases examined by Mace (1991) and Mace and Sissenwine (1993). The lower limit of τ = 0.05 used here implies a threshold fishing mortality rate exceeding F = 1 for all but two of the 11 unique M–K–t_r combinations considered (Fig. 2 and 4); the minimum was F_τ = 0.46 for the combination $M = K$=0.1, t_r = 5. Empirical estimates of τ were less than 0.05 in 9% of cases listed in Mace (1991). Thus, τ = 0.05 may not represent a lower bound for some stocks. However, it may be a reasonable lower bound to use in sensitivity analyses for cases lacking observations near the origin, since the assumption that the *S–R* relationship continues to be concave near the origin may not be valid. In multispecies systems where one species has been observed to replace another when the latter has been reduced to low levels, it is possible that the *S–R* relationship became depensatory (convex) near the origin.

In conclusion, I believe that there is no basis for rejecting values of τ within (or maybe even slightly beyond) the range 0.05 to about 0.35, a priori. Because the midpoint of this range (τ = 0.2) is similar to the average estimate of τ obtained by Mace (1991) and Mace and Sissenwine (1993), it will be used as the main reference for the remainder of the discussion.

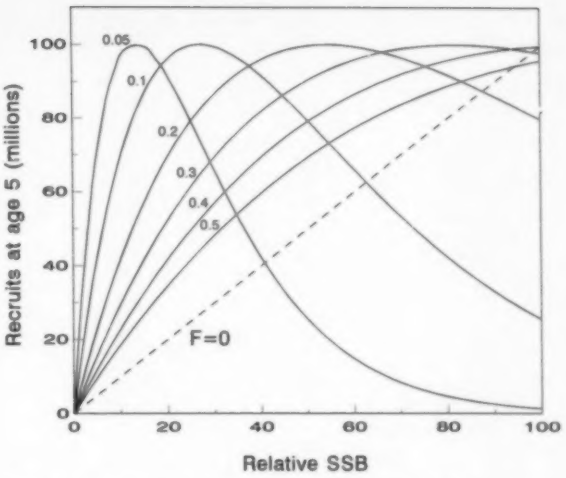

FIG. 5. Effects of τ on the shape of the Ricker *S–R* relationship (numbers above the curves are the values of τ). See legend to Fig. 1 for an explanation of the broken line.

Which BRPs Are "Best"?

The range of F_{msy} taken over all model–parameter combinations with τ in the range 0.05–0.35 was 0.029–1.46 and was always less than 47% F_τ (Fig. 2, 4, and 6). Thus, F_{msy}, the strategy that achieves the highest long-term average yield, can probably be considered "safe" for the range of parameter combinations considered here in that it falls well below F_τ. The corresponding equilibrium biomass level, B_{msy}, never crossed the commonly used threshold level of biomass of 20% B_0 (T1 in Figs. 3, 4, and 6); however, it was very close in some cases (the closest approach being 20.9%), suggesting that it should not automatically be assumed that F_{msy} is "safe" if there is reason to believe that stock productivity will be negatively impacted at levels below 20% (or more) B_0. Adoption of threshold levels higher than 20% B_0 (e.g., Quinn et al. 1990) may lead to a convergence between target and threshold levels of biomass if an F_{msy} fishing strategy is used. This appears to be less of a potential problem when recruitment dynamics are governed by the Ricker model rather than the Beverton–Holt model, because B_{msy}/B_0 was much higher and less variable for the Ricker model (Fig. 3 and 6).

The fact that F_{msy} and F_τ increase dramatically as τ decreases suggests that biomass targets and thresholds should also be dependent on the degree of compensation exhibited or assumed. Two possiblities for a threshold level of $\%B_0$ (or $\%S_0$) suggested here are to use the $\%B_0$ corresponding to 50% R_{max} based on a particular *S–R* relationship (T2 in Fig. 3, 4, and 6) or to equate the threshold percentage with τ (T3 in Fig. 3, 4, and 6). These two thresholds are similar at low τ but diverge progressively as τ increases. There is little basis for recommending one over the other, but the first could probably be used when there are sufficient data to fit

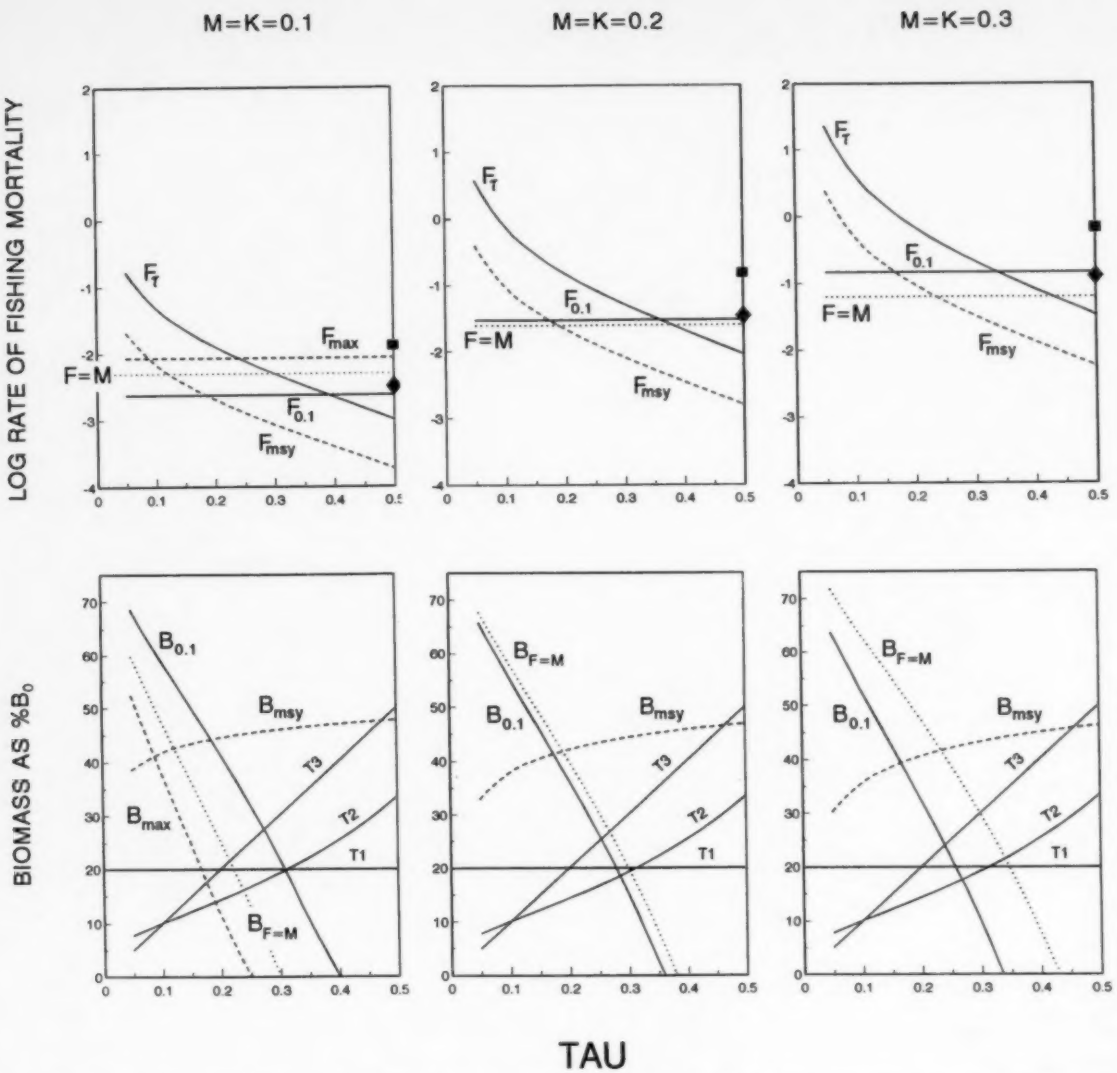

FIG. 6. Effects of various combinations of M, K, and τ on estimates of reference levels of fishing mortality (F) and equilibrium levels of biomass (B) expressed as $\%B_0$ for the Ricker S–R model. See legends to Fig. 2 and 3 for details.

an S–R relationship and the second when it is necessary to make an assumption about the likely level of compensation exhibited by a stock. Both proposed thresholds represent situations where recruitment is likely to have fallen appreciably relative to virgin or maximum levels. T2 is the point corresponding to 50% of the maximum recruitment, and T3 represents a point where, for τ in the range 0.05–0.35, recruitment has fallen to between 51 and 61% R_0 for a Beverton–Holt relationship and about 35–69% R_{max} for a Ricker relationship (Appendix B).

If F_{msy} is not known (i.e., if there are insufficient S–R data to estimate it), what is the best alternative to use with respect to achieving a compromise between approximating F_{msy} and avoiding F_τ? It has often been stated that $F = M$ is a conservative reference fishing mortality. However, for most parameter combinations, $F = M$ exceeded F_{msy}. $F = M$ was a conservative estimate of F_{msy} only when low values of τ were combined with high values of K. For $\tau = 0.2$ and $t_r = 5$, $F = M$ ranged from 35 to 66% F_τ. Therefore, it is probably reasonable to assume that $F = M$ is generally a conservative estimate of F_τ, but not necessarily a conservative estimate of F_{msy}. For some parameter combinations (low M and K, high τ), $F = M$ may be less conservative than is commonly assumed.

The advantages of using $F_{0.1}$ rather than $F = M$ are evident from Fig. 2, 4, and 6. $F_{0.1}$ incorporates the effects of the rate of growth and age of recruitment as well as natural mortality, so that it falls below M for slow-growing stocks or stocks with low age of recruitment and exceeds M for fast-growing stocks or stocks with high age of recruitment.

Similarily, reference points from SPR are likely to be superior to those from YPR because they incorporate maturity schedules in addition to the processes captured by YPR. Thus, BRPs derived from SPR take account of the effects of disparate recruitment and maturity schedules (age of 50% recruitment substantially above or below the age of 50% maturity) whereas those derived from YPR do not. Clark (1991) showed that $F_{35\%}$ and $F_{0.1}$ were generally quite close when recruitment and maturity schedules coincided but that the two diverged when there were appreciable differences between recruitment and maturity schedules. When the age of 50% maturity is less than the age of 50% recruitment, $F_{35\%}$ will generally exceed $F_{0.1}$; when the opposite is true, $F_{35\%}$ will be less than $F_{0.1}$. Therefore, strategies based on $F_{35\%}$ would result in stocks that mature before they recruit being fished much harder than stocks that recruit before they mature, whereas strategies based on $F_{0.1}$ would not distinguish between the two situations.

Given that (i) $F_{35\%}$ generally exceeded $F_{0.1}$ for the parameter combinations considered here (in which the ages of recruiment and maturity were always equal), (ii) $F_{0.1}$ averaged about $F_{38\%}$ for the empirical estimates obtained by Mace (1991) and Mace and Sissenwine (1993), and (iii) $F_{35\%}$ and $F_{0.1}$ both invariably exceeded F_{msy} at $\tau = 0.2$ for all the model–parameter combinations used here, I suggest a default fishing target of at least $F_{40\%}$ as a robust approximation to F_{msy} that will not exceed F_τ unless τ exceeds 0.4. This is similar to the default of $F_{35\%}$ suggested by Clark (1991) who showed that fishing at $F_{35\%}$ would achieve at least 75% of MSY for a wide range of deterministic *S–R* relationships. It is also identical to the recommendation he later made after extending his deterministic analysis by adding recruitment variability (Clark 1993). For the reasons given here and in Clark (1993), I suggest that $F_{40\%}$ represents a modest improvement over $F_{35\%}$.

F_{max} always exceeds F_{msy} for a Beverton–Holt *S–R* function, but F_{msy} may exceed F_{max} at low τ for the Ricker function (Fig. 6). The fact that F_{max} is generally larger than F_{msy} except when the *S–R* relationship is dome shaped and has strong density dependence is already well known (e.g., Deriso 1982). For the model–parameter combinations considered here, F_{max} was always above or only slightly below F_τ at $\tau = 0.2$ (Fig. 2, 4, and 6). This suggests that while F_{max} may often be too high as a target, it may sometimes be a useful threshold. Given that (i) BRPs based on SPR should generally be considered superior to those based on YPR, (ii) F_{max} is often not defined (whenever the instantaneous rate of growth exceeds the instantaneous rate of natural mortality), and (iii) F_{max} averaged about 21% SPR in the studies by Mace (1991) and Mace and Sissenwine (1993), it may be useful to consider a fishing mortality rate of about $F_{20\%}$ as a threshold for stocks that are reasonably certain to have at least "average" resilience. However, $F_{20\%}$ corresponds to the extinction threshold for $\tau = 0.2$; thus, it will not be sustainable over the upper half of the range $\tau = 0.05$–0.35. In the absence of adequate information on stock dynamics, a more prudent approach is to use a default overfishing threshold of $F_{30\%}$, as suggested by Mace and Sissenwine (1993). A threshold of $F_{30\%}$ has also been recommended by Thompson (1993) based on an examination of the dynamics of stocks where the *S–R* relationship is represented by a depensatory form of the Beverton–Holt function.

Dependence of Results on Input Assumptions

This study shows that the validity of various reference levels of F as approximations to F_{msy}, or as thresholds of overfishing, is highly dependent on life history characteristics. The sensitivity of F_τ and F_{msy} to the life history parameters considered here increased through the sequence K, M, τ. Ironically, the difficulty of estimating these three parameters increases in the same sequence. Choice of τ and the validity of F_τ as an estimate of the extinction threshold is particularly problematic. In reality, F_τ is almost always derived by extrapolating beyond the observations. The assumption that the survival ratio is maximized as S approaches zero ignores the observation that stocks reduced to low levels frequently "collapse", in the sense that they remain at low biomass for long periods of time. Stocks may collapse long before F reaches F_τ. Nevertheless, F_τ may be useful as a boundary condition, indicating the ultimate consequences of assuming or estimating particular levels of compensation.

This study also shows that the results are sensitive to the form of the *S–R* relationship. For *S–R* functions with maximum slope occurring at the origin, F_τ will always be given by an expression similar to equation (15); i.e., F_τ is the value of F that satisfies the expression SPR = the inverse of the slope at the origin. Thus, for a given set of life history parameters, F_τ values for Beverton–Holt and Ricker *S–R* functions are identical. For *S–R* functions that have maximum slope at $S > 0$ (e.g., those that are convex near the origin), F_τ will be associated with a nonzero equilibrium biomass. Even when F_τ values are similar, F_{msy} values may diverge considerably; F_{msy} estimates based on the Ricker model (Fig. 6) were as much as 2.3 times those based on the Beverton–Holt model (Fig. 2). For the same maximum R and slope at the origin relative to the no-fishing replacement line, the Ricker model represents a much more productive fish stock in terms of the excess of recruitment over the replacement level required in the absence of fishing (Figs. 1 and 5). Not only was F_{msy} consistently higher, so too were the corresponding levels of MSY, B_{msy} (except at τ =0.05 and 0.1), and B_{msy} as a percentage of B_0.

Extensions to Stochastic Systems

Deterministic models provide a simplified approach that represents a useful first step towards identifying potential pitfalls of proposed control laws for stochastic systems. In addition, depending on the skewness of the distributions used in the stochastic system, the deterministic results may often be close to the average or median of the stochastic results.

Part of the impetus for this study was the increasingly common usage of a threshold biomass level of 20% B_0. For the Beverton–Holt model, low τ and high K and age of recruitment result in B_{msy} approaching the 20% B_0 threshold (T1 in Fig. 3 and 4). Thus, a control law that restricted $P(B < 20\%\ B_0)$ to some upper limit would have a greater tendency to reject F_{msy} the more productive and robust the system. Worse yet, this control law would give increasingly conservative estimates of the optimum F as the age of recruitment was increased within a stock. It makes more sense to treat stocks differentially based on the relative degrees of resilience and/or productivity they exhibit. Either of the two recommendations suggested in this paper (the two thresh-

olds, T2 and T3, superimposed on Fig. 3, 4, and 6) could be used as the basis of control laws for stochastic systems. For example, the optimum F might be specified as that F that provides the closest approximation to F_{msy} subject to the constraint that $P(B < 100{\cdot}\tau{\cdot}B_0) < 5\%$ (or less, since thresholds based on the slope at the origin or 50% R_{max} are unlikely to be conservative and should probably be treated as nearly as possible as absolute boundaries not to be crossed). The frequency at which B is likely to fall below such thresholds can be assessed qualitatively from diagrams like Fig. 3, 4, and 6. It may even be possible to use deterministic results to rank parameter combinations in terms of the relative probabilities of violating the thresholds, without resorting to stochastic simulations.

Conclusions and Recommendations

The merits of one BRP over another depend on a number of factors including life history characteristics (e.g., M, K, τ), whether or not or how well these are known, and the perceived importance of the risk of driving a stock below some minimum threshold level relative to the risk of sacrificing yield. In the common situation where there is adequate information to place bounds on all relevant life history parameters except those characterizing the *S–R* relationship, I recommend using a default target fishing mortality rate of $F_{40\%}$ and a default overfishing threshold SSB given by $\%S_0 = 100\tau$ as a basis for formulating risk-averse fishing strategies when the two types of risk are given similar weighting. $F_{40\%}$ is similar to $F_{0.1}$ when recruitment and maturity schedules coincide, approximates F_{msy} for τ in the range of about 0.05–0.2, and does not exceed F_τ unless $\tau > 0.4$. The proposed threshold SSB corresponds to a drop in recruitment to around half the virgin or maximum level for a wide range of parameterizations of both the Beverton–Holt and Ricker *S–R* functions (actual range about one third to two thirds; Appendix B).

The biggest problem is the choice of τ. By definition, τ determines the threshold fishing mortality. Therefore, speculation about the likely range of τ will have a direct influence on conclusions about the best choice for the threshold F. The current theoretical study does not provide a basis for altering the previous recommendation by Mace and Sissenwine (1993), who suggested using $\tau = 0.2$ as a default overfishing threshold for stocks believed to have at least average resilience and $\tau = 0.3$ as a threshold for little-known stocks. These values of τ would correspond to threshold biomass levels of 20% S_0 and 30% S_0, respectively (or the same $\%B_0$ values, if B_0 is equivalent to S_0). However, there is a need to be cautious in the application of the less-conservative default threshold. The corresponding threshold fishing mortality ($F_{20\%}$)will exceed the extinction threshold (F_τ) if $\tau > 0.2$. In fact, if τ is believed to be near 0.2, it is probably unwise to use a threshold F as high as $F_{20\%}$, since thresholds sometimes have a tendency to become targets. Currently, $F_{20\%}$ is being adopted as a default overfishing threshold (and sometimes even a fishing target) in an increasing number of fisheries management plans in the United States. Of course, for stocks known or believed to have extremely high resilience, $F_{20\%}$ may be a conservative threshold.

If the *S–R* relationship is known, there is no need to use defaults, since F_{msy} and other BRPs can be estimated directly. If the relationship can be fitted by an asymptotic or domed *S–R* function and there are adequate observations at low stock size, I suggest using the slope at the origin as a threshold F and the SSB corresponding to 50% R_{max} as a threshold biomass. Note, however, that these thresholds hardly represent conservative reference points, and so should generally be treated as absolute thresholds in the sense that the probability of crossing them should be vanishingly small.

If there are insufficient observations to characterize the *S–R* function over its entire range, the observed survival ratios can be used to estimate the replacement F (F_{rep}) in the manner outlined by Sissenwine and Shepherd (1987) and Gabriel et al. (1989) and implemented by Mace (1991) and Mace and Sissenwine (1993). The average (or median) observed survial ratio can then be used as the basis for a threshold F if it is believed that the stock is dangerously low, or well below historic observations, or as a target F if the observations have been collected from a fishery operating at near-optimal levels.

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Appendix A. Relationship between YPR and MSY for Beverton–Holt and Ricker *S–R* Functions

The following equations apply to the special case where recruitment and maturity schedules coincide so that the age of recruitment (t_r) equals the age of maturity (t_m) and the average recruited biomass per recruit (BPR) equals the average spawning biomass per recruit (SPR).

For the case of knife-edge recruitment, the yield per recruit (YPR) equation is given by

$$\text{(A1)} \qquad \text{YPR} = F\left(\frac{1-e^{-(F+M)}}{F+M}\right)\sum_{t=t_r}^{\infty}\left(N_t\ e^{-(F+M)(t-t_r)}\ W_t\right)$$

where

$N_t = 1$ at $t=t_r$.

Substituting from equation (5) leads to simple relationships between YPR and SPR:

$$\text{(A2)} \qquad \text{YPR} = F\cdot\text{SPR}$$

and between SPR and the slope at the origin of the YPR relationship:

$$\text{(A3)} \qquad \left.\frac{d(\text{YPR})}{dF}\right|_{F=0} = \left(\frac{1-e^{-M}}{M}\right)\sum_{t=t_r}^{\infty}\left(N_t\ e^{-M(t-t_r)}\ W_t\right),$$

$$= \text{SPR}_{F=0}.$$

Thus, $F_{0.1}$ is the fishing mortality rate that satisfies the relationship

$$\text{(A4)} \qquad \frac{d(\text{YPR})}{dF} = 0.1\cdot\text{SPR}_{F=0}.$$

For the Beverton–Holt *S–R* model, F_{msy} is the fishing mortality rate, F', that maximizes the expression (equation (13))

$$X = F'\cdot(\text{SPR}_{F'} - \alpha).$$

Substituting from equations (A2) and (8) results in

$$\text{(A5)} \qquad X = \text{YPR}_{F'} - F\cdot\tau\cdot\text{SPR}_{F=0}.$$

Differentiating (A5) with respect to F and setting $dX/dF=0$ gives

$$\text{(A6)} \qquad \frac{d(\text{YPR})}{dF} = \tau\cdot\text{SPR}_{F=0}.$$

Thus, from equations (A4) and (A6), $F_{msy} = F_{0.1}$ for the special case $\tau = 0.1$, $F_{msy} > F_{0.1}$ for $\tau < 0.1$, and $F_{msy} < F_{0.1}$ for $\tau > 0.1$.

These results can be generalized to the case where recruitment and maturity are not knife-edge; equations (A3), (A4), and (A6) will hold as long as the recruitment and maturity ogives are the same.

For the Ricker relationship, F_{msy} is the fishing mortality rate, F', that maximizes (equation (17))

$$X = F'\cdot\log_e(\alpha\cdot\text{SPR}_{F'}).$$

Using the same procedure as above gives a somewhat more complex relationship between MSY and YPR. F_{msy} is the fishing mortality rate that maximizes

$$\frac{d(\text{YPR})}{dF} = \frac{\text{YPR}}{F}\left[1-\log_e\left(\frac{\text{YPR}}{F\cdot\tau\cdot\text{SPR}_{F=0}}\right)\right].$$

Thus, $F_{0.1} = F_{msy}$ when

$$0.1\cdot\text{SPR}_{F=0} = \frac{\text{YPR}}{F}\left[1-\log_e\left(\frac{\text{YPR}}{F\cdot r\cdot\text{SPR}_{F=0}}\right)\right].$$

Deriso (1987) provided a more detailed exploration of the relationship between $F_{0.1}$ and F_{msy} for the Ricker model.

Appendix B. Relationship between $\%B_0$ and Threshold %SPR for Beverton–Holt and Ricker *S–R* Relationships

Threshold levels of %SPR (SPR expressed as a percentage of $\text{SPR}_{F=0}$) are commonly equated with threshold levels of $\%B_0$ (e.g., a threshold of 20% SPR is used interchangeably with 20% B_0). However, if the threshold %SPR is the %SPR associated with the slope at the origin of the spawning–recruitment (*S–R*) relationship (equation (7)), it is obvious that the two do not equate because the corresponding equilibrium biomass is zero. The translation between the two depends on the shape of the underlying *S–R* relationship. An alternative threshold based on relative recruitment is defined here and used as a reference point for comparing levels of $\%B_0$ and threshold %SPR.

The suggested alternative threshold is the biomass level corresponding to 50% of the maximum recruitment estimated from a fitted *S–R* relationship (50% R_{max}). It makes sense to base threshold definitions on relative recruitment because one of the main reasons for choosing a non-zero biomass threshold is the belief that low biomass leads to an increased probability of "recruitment failure" or an average level of recruitment that is so low that stock rebuilding is impeded. The 50% level is arbitrary, but there is likely to be general agreement that stocks should not be permitted to fall below a biomass level that would produce an average recruitment of 50% of the expected maximum.

The following equations define γ, ζ, and τ, which are the threshold levels (proportions) of B_0 (here equivalent to S_0), R_{max}, and $\text{SPR}_{F=0}$, respectively:

$$S = \gamma B_0;\ 0 < \gamma < 1$$

$$\text{(B1)} \qquad R = \zeta R_{max};\ 0 < \zeta < 1$$

$$\left.\frac{dR}{dS}\right|_{S=0} = \frac{1}{\tau\cdot\text{SPR}_{F=0}} = \frac{1}{\tau\cdot(B_0/R_0)};\ 0 < \tau < 1$$

where S = spawning biomass, B_0 = virgin recruited biomass = virgin spawning biomass ($=S_0$), R = recruitment in numbers, R_{max} = maximum expected recruitment, and τ = the ratio between the slope corresponding to $\text{SPR}_{F=0}$ (i.e., $1/\text{SPR}_{F=0}$ or R_0/B_0) and the slope at the origin ($dR/dS_{(S=0)}$); thus, τ = the threshold %SPR expressed as a proportion.

These equations are used in conjunction with the Beverton–Holt and Ricker *S–R* functions (i) to calculate the $\%B_0$ corresponding to 50% R_{max} for various levels of threshold %SPR (i.e., to find γ when $\zeta = 0.5$ with τ known) and (ii) to calculate the $\%R_{max}$ resulting from the common assumption that $\%B_0$ is equivalent to the threshold %SPR (i.e., to find ζ when $\gamma = \tau$).

TABLE B1. Relationships between $\%B_0$, threshold %SPR, and $\%R_{max}$ (γ, τ, and ζ, respectively, expressed as percentages).

Critical point = 50% R_{max} (ζ = 0.5)			$\%B_0$ = threshold %SPR ($\gamma = \tau$)		
Threshold %SPR (100τ)	$\%B_0$ (100γ)		Threshold %SPR (100τ)	$\%R_{max}$ (100ζ)	
	Beverton–Holt	Ricker		Beverton–Holt	Ricker
5	4.8	7.8	5	51.3	35.1
10	9.1	10.1	10	52.6	49.7
20	16.7	14.4	20	55.6	63.4
30	23.1	19.3	30	58.8	68.4
40	28.6	25.3	40	62.5	69.1
50	33.3	33.5	50	66.7	66.6

1. Beverton–Holt *S–R* Relationship with $R_{max} = 1/\beta$.

The Beverton–Holt *S–R* relationship is given by

$$R = \frac{S}{\alpha + \beta S} \tag{B2}$$

where α and β are parameters that define the maximum of the function and the slope at the origin by

$$\lim_{S \to \infty} R = 1/\beta = R_{max} \tag{B3}$$

$$\left.\frac{dR}{dS}\right|_{S=0} = \frac{1}{\alpha}. \tag{B4}$$

Equations (B1) and (B4) result in

$$\alpha = \tau \frac{B_0}{R_0}. \tag{B5}$$

Combining equations (B1)–(B3) and (B5) gives

$$\begin{aligned} &\gamma = \tau \text{ when } \zeta = 0.5 \\ &\zeta = 0.5 \text{ when } \gamma = \tau. \end{aligned} \tag{B6}$$

2. Beverton–Holt *S–R* Relationship with R_{max} Given by the Intersection of the *S–R* Curve with the Line $R = (1/\mathrm{SPR}_{F=0}) \cdot S$ (i.e., $R_{max} = R_0$ is a Point on the Curve)

An expression for β is obtained by sustituting the point (B_0, R_0) and equation (B5) into equation (B2):

$$\beta = \frac{1 - \tau}{\tau^2 R_0}. \tag{B7}$$

It follows from equations (B1), (B2), (B5), and (B7) that

$$\begin{aligned} &\gamma = \frac{\tau}{1 + \tau} \text{ when } \zeta = 0.5 \\ &\zeta = \frac{1}{2 - \tau} \text{ when } \gamma = \tau. \end{aligned} \tag{B8}$$

At $\zeta = 0.5$, γ and τ are reasonably close as long as τ is less than about 0.2 (Table B1). When $\gamma = \tau$ and τ is in the range 0–0.35, ζ will be in the range 0.5–0.61. When (B_0, R_0) is a point on the curve defined by equation (B5), equation (B6) is a limiting case for equation (B8), occurring when $\gamma = \tau$ approaches 0.

3. Ricker *S–R* Relationship with R_{max} Given by the Maximum of the Function and R_0 Given by the Intersection of the *S–R* Curve with $R = (1/\mathrm{SPR}_{F=0}) \cdot S$ (i.e., (B_0, R_0) is a Point on the Curve and $R_0 \leq R_{max}$)

The Ricker *S–R* relationship is given by

$$R = aSe^{-bS} \tag{B9}$$

where a and b are parameters that define the maximum of the function and the slope at the origin by

$$\frac{dR}{dS} = 0 \Rightarrow S = \frac{1}{b};\ R_{max} = \frac{a}{b} e^{-1} \tag{B10}$$

$$\left.\frac{dR}{dS}\right|_{S=0} = a. \tag{B11}$$

Equations (B1) and (B11) imply that

$$a = \frac{R_0}{\tau B_0}. \tag{B12}$$

Combining equations (B1), (B9), (B10), and (B12) gives

$$\zeta = \frac{\gamma}{\tau} \frac{R_0}{R_{max}} e^{-(\gamma/\tau) \cdot (R_0/R_{max}) \cdot e^{-1}}. \tag{B13}$$

Thus, γ must be found by iteration. For the case $\zeta = 0.5$, the divergence between γ and τ is somewhat greater for the Ricker function than for the Beverton–Holt function (Table B1). For $\gamma = \tau$ in equation (B13), $\zeta = (R_0/R_{max}) \cdot e^{-(R_0/R_{max}) \cdot e^{-1}}$. The range covered by ζ in this case exceeds the range calculated for the Beverton–Holt relationship (Table B1). For R_0 in the range 0.5–1.0 R_{max} in equation (B13), ζ will be in the range 0.42–0.69.

In conclusion, for these common *S–R* functions, the level of $\%B_0$ ($\%S_0$) that equals the threshold %SPR defined by the ratio between the slope at $\mathrm{SPR}_{F=0}$ and the slope at the origin will correspond to an expected recruitment level that is appreciably below the maximum. For reasonable ranges of the threshold %SPR (0.05–0.35), the expected recruitment corresponding to $\%B_0$ = threshold %SPR will range from 51 to 61% R_0 for the Beverton–Holt function and from 35 to 69% R_{max} for the Ricker function.

Vertical Distribution of Northern Shrimp (*Pandalus borealis*) Larvae in the Gulf of St. Lawrence; Implications for Trophic Interactions and Transport[1]

Patrick Ouellet and Denis Lefaivre

Ministère des Pêches et des Océans, Institut Maurice-Lamontagne, 850 route de la mer, Mont-Joli, PQ G5H 3Z4, Canada

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In the northwestern Gulf of St. Lawrence in spring 1987 and 1988, stage I and II northern shrimp (*Pandalus borealis*) larvae were concentrated in the upper (<30 m) layers above the permanent pycnocline and coincident with subsurface chlorophyll *a* and suspended particle concentration maxima; this was above other macrozooplankton taxa in the daytime. Shrimp larvae maintained their vertical position relative to the maximum density gradient in the water column in daytime but moved towards the surface at night. Estimation of larval residual transport (~66 km) during the first developmental stage (12 d) corresponded to the horizontal scale of patches of stage I shrimp larvae in the northwest sector of the Gulf. The result is consistent with the suggestion of localized and short-duration larval emergence in the sector. The direction of mass transport and current speed were similar throughout the upper layers of the water column; consequently, the direction and magnitude of larval shrimp transport were not dependent on their vertical position. We suggest that the vertical distribution maintained by shrimp larvae is a mechanism to ensure maximum food availability and to optimize development time in the stratified water of the northwestern Gulf of St. Lawrence.

Au printemps 1987 et 1988 dans le nord-ouest du golfe du Saint-Laurent, les zoées I et II de crevette nordique (*Pandalus borealis*) étaient concentrées dans la couche supérieure (< 30 m), au-dessus de la pycnocline permanente et coïncidant avec les maxima de chlorophylle *a* et de matières en suspention sous la surface; au-dessus des autres taxons de macrozooplancton pendant le jour. Les larves maintiennent leur position verticale relative au maximum du gradient de densité dans la colonne le jour et se déplacent vers la surface la nuit. Le transport résiduel des larves a été estimé à ~66 km pour la durée du premier stade de développement (12 jours), ce qui correspond à la dimension horizontale des aggrégations de larves de stade I dans le secteur nord-ouest du Golfe. Le résultat supporte la proposition d'une émergence brève et localisée de larves de crevette dans le secteur. La direction du transport et la vitesse du courant étaient semblables au-dessus de 50 m. En conséquence, l'amplitude et la direction du déplacement des larves n'étaient pas dépendent de leur position verticale. Nous proposons que la distribution verticale des larves représente un mécanisme assurant la disponibilité de nourriture et optimise le temps de développement dans la colonne d'eau stratifiée du nord-ouest du golfe du Saint-Laurent.

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Survival variability during the larval stages is believed to be responsible for interannual variation in recruitment in marine fish and invertebrate populations (Hjort 1926; Cushing 1975). Two major sources of variability are often proposed in the fisheries oceanography literature: (1) processes based on trophic interactions, i.e., starvation/predation effects, and (2) unfavorable dispersal through advective transport during pelagic development (Hjort 1926; Cohen et al. 1988). In practice, the influence of both factors can be modulated through a single phenomenon, the vertical distribution of the larval stages relative to the physical structure of the water column.

Various patterns of vertical distribution have been documented for decapod larvae, with vertical diel migrations and ontogenic variations being the main features (Haynes 1983; Lindley 1986). The vertical position of larvae and the structure of the water column could affect (1) prey encounter probabilities in terms of suitable size and concentration (Lasker 1975) and nutritional value (Napp et al. 1988b) and (2) co-occurrence of the larvae with predators and competitors (Fortier and Harris 1989). Vertical variations in the direction and magnitude of the current field can also determine the importance of transport and dispersal during pelagic development and potentially affect recruitment to the local populations (Fortier and Leggett 1982; Rothlisberg 1982; Rothlisberg et al. 1983; McConaugha 1988).

The first pelagic larval stage (a free-swimming and actively feeding zoea: 5–6 mm total length) of northern shrimp (*Pandalus borealis*) appears in April – early May in the water of the Gulf of St. Lawrence (Ouellet et al. 1990). Pelagic development entails five to six stages and can last

[1]Contribution to the COHJAC (Circulation, Oceanography, and Hydrography of the strait of Jacques Cartier) Program.

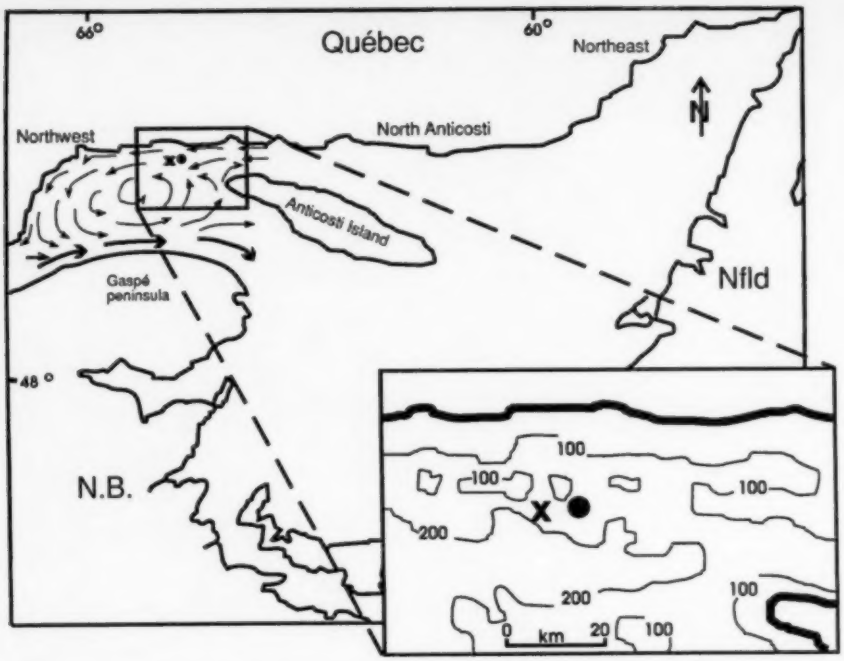

FIG. 1. General circulation in the northwest sector of the Gulf of St. Lawrence and bathymetric details of the zooplankton sampling site (×) and position of the current meter mooring (●).

3 mo at 5°C (Shumway et al. 1985). Shrimp larvae are generally encountered within the upper layers (<50 m) of the water column, and high concentrations of planktonic food items (diatoms, copepods developmental stages, etc.) was argued to be an important factor in the success of the early larval stages (see Shumway et al. 1985). The structure and scale of the horizontal distribution of *P. borealis* larvae in the northern Gulf of St. Lawrence have been described in relation to the hydrography of the region (Ouellet et al. 1990). Emergence and persistence of the first pelagic developmental stages were reported in the different hydrographic sectors of the northern Gulf. However, within each sector, there was no clear relationship between the spatial hydrographic heterogeneity and that of the larval (stage II and later) abundance distribution. It was therefore hypothesized that differential mortality and developmental rates in response to ecological variability within the sectors could explain the spatial pattern of shrimp larval abundance distribution (Ouellet et al. 1990). A test of that hypothesis would require the determination of the principal ecological factors affecting larval development and possibly survival in the water column in comparison with the potential for larval transport in the northern Gulf of St. Lawrence.

In this study the vertical distribution of shrimp larvae in the northwest sector of the Gulf is presented. The objectives of sampling were (1) to describe the vertical distribution of the early larval stages of shrimp in relation to the physical structure of the water column and other components of the zooplankton community and (2) to assess the potential influence of the vertical structure of the local circulation on the direction and magnitude of early larval transport.

Materials and Methods

Sampling Site and Sampling Protocol

When averaged seasonally and over the entire area, the circulation in the Gulf of St. Lawrence is described as estuarine-like and cyclonic near the surface (Koutitonsky and Bugden 1991). For the northwest sector of the Gulf, an offshore pressure gradient along the Quebec north shore created by lateral runoff induces a coastal current (5–10 $cm \cdot s^{-1}$) towards the west (Koutitonsky and Bugden 1991). Together, the westward circulation along the coast and the St. Lawrence River outflow along the Gaspé Peninsula (Gaspé coastal jet current) compose another important feature of the circulation in the northwest sector: a partially wind-forced, quasi-permanent geostrophic cyclonic eddy west of Anticosti Island (El-Sabh 1976; Koutitonsky and Bugden 1991) (Fig. 1).

Typical (summer) temperature – salinity profiles in the northern Gulf reveal a highly stratified water column with (1) a surface layer (0–30 m, salinity from 27 to 32), (2) a cold intermediate layer (30–125 m, −1 to −2°C, salinity from 31.5 to 33), and (3) a deep layer (4–6°C, salinity >34) of typical Atlantic and Scotian Shelf waters (Koutitonsky and Bugden 1991). During the winter, surface cooling and vertical convection homogenize the water column and the cold layer extends to the surface (Bugden et al. 1982). In the spring, an increase in surface fluxes (i.e., freshwater runoff, solar radiation) initiates the seasonal stratification of the water column. The increasing stratification during the spring reduces the amplitude of coastal upwelling and the vertical exchange between the surface and the deeper layers (Bugden 1981); another consequence is a decoupling of the

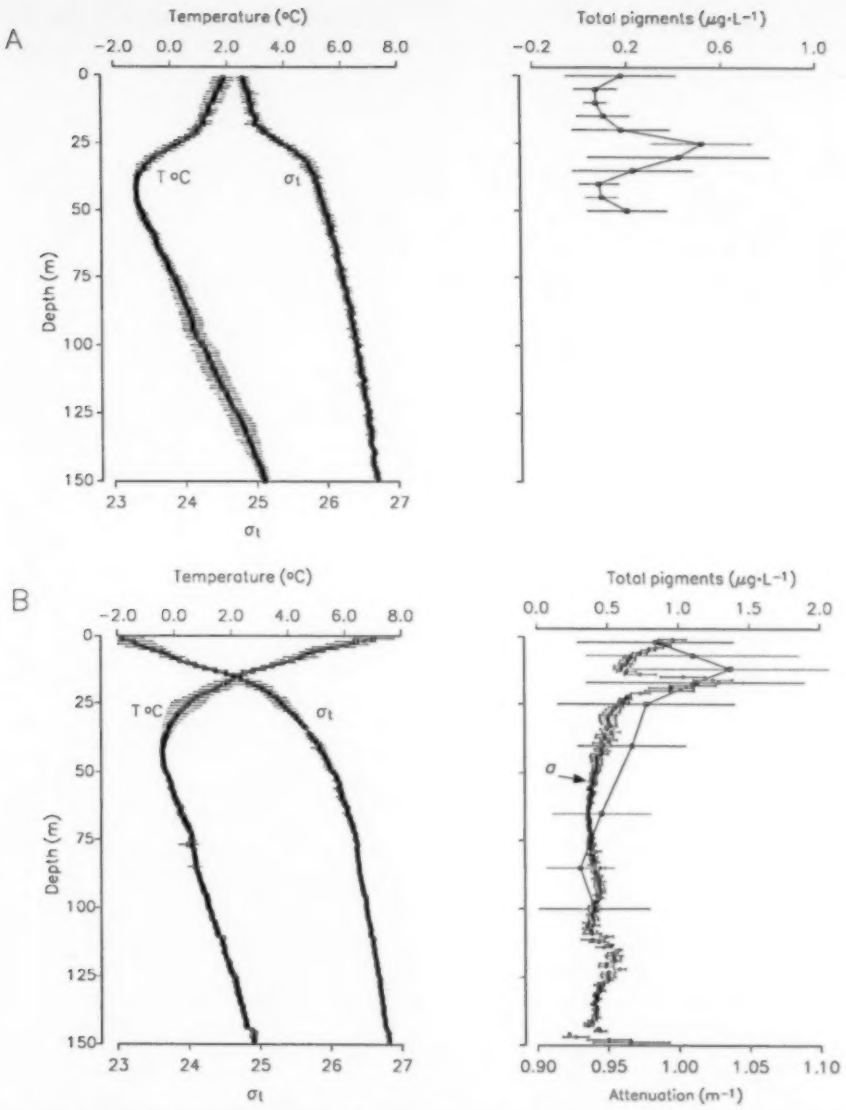

FIG. 2. Depth profile of temperature and density (σ_t) and total pigment concentration and light attenuation a for (A) the 44-h series of May 1987 and (B) the 32-h series of May 1988. Values are means ± 1 SD.

surface (0–20 m) from the deep-layer circulation (Bugden 1981).

Biological and physical oceanographic sampling was conducted at a coastal site in the northwest sector of the Gulf in an area where high concentrations of larval shrimp were found in May 1987 (Ouellet et al. 1990). The study site was between the 100-, and 200-m isobaths over a zone of complex bathymetry, featuring a series of shallow (≤100 m) banks north of the site (Fig. 1).

Zooplankton sampling was carried out at a fixed station (50°00′N, 065°20′W; Fig. 1) on two occasions: (1) 1987, from 5 May (05:00 a.m. (EDT)) to 7 May (01:00 a.m. (EDT)) for a 44-h series, and (2) 1988, from 21 May (03:00 a.m. (EDT)) to 22 May (11:00 a.m. (EDT)) for a 32-h series. For both series, nine discrete depth strata (0–5, 5–10, 10–15, 15–20, 20–30, 30–50, 50–75, 75–100, and 100–150 m depth intervals) were sampled every 2 h using an automated multiple-net sampler (BIONESS; Sameoto et al. 1980). The gear was equipped with nine nets (333-μm mesh size) of 1 m^2 opening, inside and outside digital flowmeters, a pressure gauge, and temperature and salinity sensors. Opening and closing of the nets were controlled remotely using an onboard computer. Sampling proceeded from the deepest (100–150 m) stratum toward the surface and the duration of each set (i.e., the nine strata combined) ranged from 30 to 45 min. Sawtooth oblique tows were conducted within each stratum for 3–5 min, and on average, 400 m^3 of water was filtered per net. During the May 1988 sampling series, a Sea Tech 25-cm

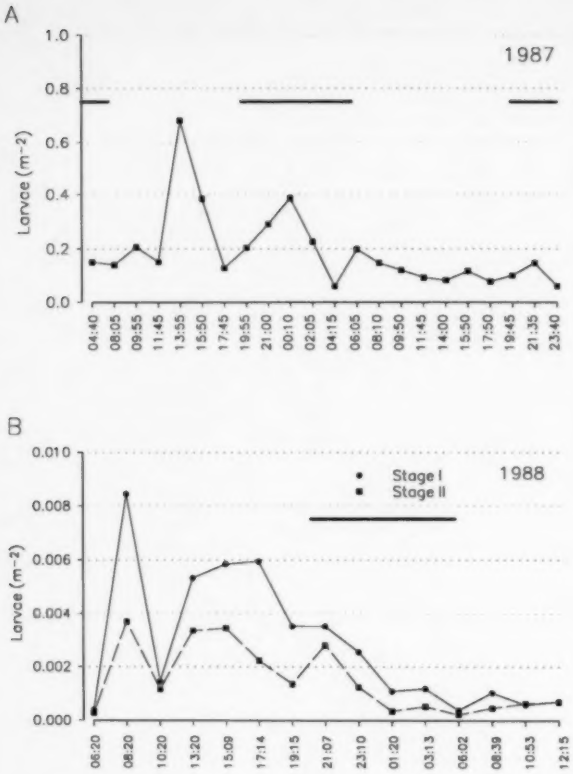

FIG. 3. Total abundance of shrimp larvae (integrated over all stratum) in each set during each of the (A) May 1987 and (B) May 1988 sampling series. Time of day (EDT) indicates the end of each BIONESS set, and the horizontal lines represent nighttime.

beam transmissometer (660 nm) was added to the sampler for in situ light attenuation measurements to be used as an index of suspended particle concentration in the water column (Kiefer and Austin 1974; Vandevelde et al. 1988).

During both series, water samples were collected for determination of total pigments (chlorophyll *a* and phaeopigments). In 1987, following the zooplankton sampling, samples were obtained at 5-m intervals from 0 to 50 m with an array of 5-L Niskin bottles. In 1988, water samples were obtained at middepth in each stratum (100 m maximum) for comparison with light attenuation data.

The sampling station was located near a current meter mooring in May 1987 (Fig. 1). Aanderaa model RCM-4-S current meters were moored at depths of 20, 50, and 95 m (in 100 m of water) and recorded for 30 d (2 May – 1 June) at a sampling interval of 30 min.

Data Analyses

Each BIONESS sample was sorted for decapods, fish larvae, and macrozooplankton (euphausiids, chaetognaths, and scyphozoans (hydrozoans)). The remaining sample was then drained on a 250-μm screen and total zooplankton (>250 μm) biomass (millilitres per cubic metre) was estimated by displacement volume. Shrimp larvae and macrozooplankton abundance were converted to concentration (number per cubic metre) for each depth stratum according to the volume filtered by each net. Shrimp larvae were staged according to Haynes (1979), and total and carapace lengths were measured under a dissecting microscope.

The vertical distributions of decapod larvae (including *P. borealis*) and macrozooplankton taxa were determined by estimating the centre of mass of the distributions for each sampling series (Fortier and Leggett 1982; Frank and McRuer 1989):

$$Z_{\mathrm{cm}_k} = \sum_{i=1}^{9} p_i \cdot Z_i$$

where Z_{cm_k} is the depth (metres) of the centre of mass of taxon k, p_i is the proportion of the taxon in stratum i, and Z_i is the midpoint in the stratum (i.e., 2.5, 7.5, 12.5, 17.5, 25, 40, 62.5, 87.5, and 125 m, respectively). The significance of day and night effects on the position of the centre of mass of *P. borealis* larvae was assessed using the Runs test (Sokal and Rohlf 1981).

Chlorophyll *a* and phaeopigment concentrations at depth were estimated onboard using a whole-water extraction procedure (Phinney and Yentsch 1985; Fréchette and Grant 1991). Two 500-μL subsamples from each (unfiltered) water sample were extracted in the dark in 4.5 mL of cold acetone in 12 × 75 mm borosilicate tubes at 4°C for 24 h. The extract was centrifuged and fluorescence determined on a Turner model 111 fluorometer equipped with a high-sensitivity door; the two measurements were averaged.

Underwater light transmission was used to estimate the attenuation coefficient *a* (per metre):

$$a = \frac{-(\ln(T))}{0.25}$$

where T is the relative transmission at depth and 0.25 m is the length of the light path for the instrument (Lieberman et al. 1984).

A low-pass filter was applied to the current meter data to estimate advection over periods longer than the tidal signal, i.e., the filter attenuates any signal of frequency higher than 35 h. The analysis distinguishes between the residual and the mean current where the residual current is the vectorial summation of the current speed and direction over the periods of interest (3 and 27 d) and the mean current is the summation of the speed over the same intervals divided by the number of observations. If the current were always flowing in the same direction, the residual and the mean currents would be the same. Consequently, when the mean current is different from the residual current, this implies a change in direction of the current during the interval.

Results

Stratification in the water column was different for the two years of sampling. In 1987, a relatively deep (~20 m), partially mixed layer was observed with a distinct pigment maximum which coincided with the pycnocline (Fig. 2A). In 1988, the surface water was warmer and there were stronger surface temperature and density gradients following the seasonal progression (e.g., freshwater runoff, solar radiation) in the northwest Gulf, but the maxima in pigment concentration and light attenuation occurred above the cold intermediate layer as in 1987 (Fig. 2B). However, during each

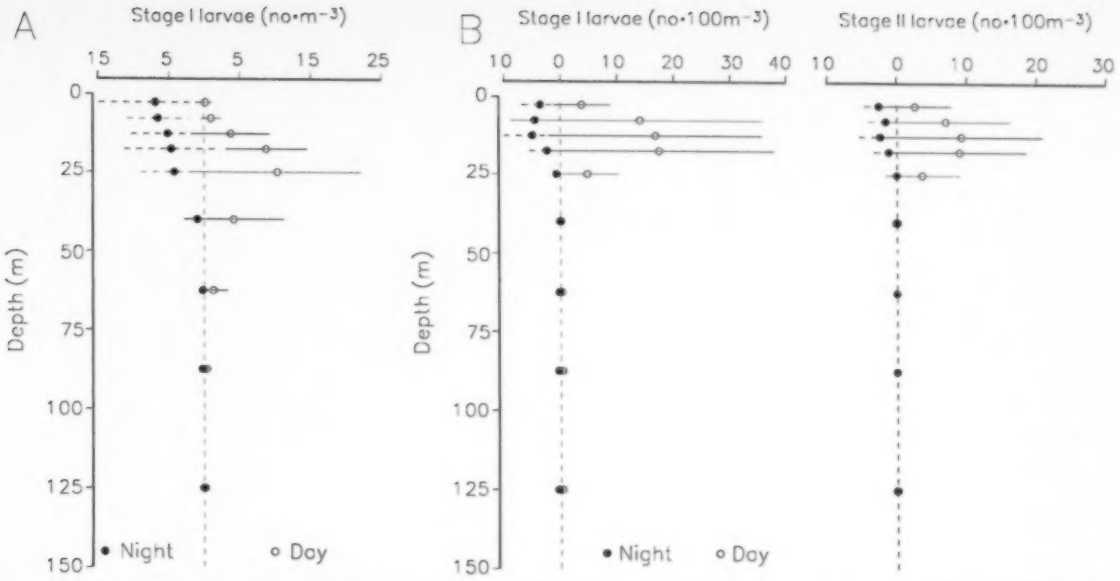

FIG. 4. Mean density of shrimp larvae (±1 SD) per stratum for day (○) and night (●) sets of the (A) May 1987 and (B) May 1988 series.

zooplankton sampling series the water mass at the sampling site was horizontally homogeneous as shown by the low variability of the averaged temperature and density (σ_t) profiles for each period (Fig. 2).

Pandalus borealis larvae represented 72 and 30%, for 1987 and 1988, respectively, of all decapod larvae sampled at the site. Only stage I shrimp larvae were present during the 1987 sampling series; total concentration (i.e., integrated over all strata; number per square metre) varied among sets (Fig. 3A). Two maxima (14:00, 5 May, and 00:00, 6 May) were observed during the first 24 h, after which total larval concentration remained relatively constant (Fig. 3A). Stage I and II shrimp larvae were present during the 1988 sampling series; larval concentration progressively declined with time (Fig. 3B). Both stages showed a similar pattern of abundance fluctuations, suggesting a relatively constant proportion of each stage in most sets. In both years, no systematic effects of day and night sampling on total larval abundance could be deduced from the time series of larval concentration.

Vertical Distribution of Shrimp Larvae and Its Relationship with the Zooplankton Community

The vertical distribution of larvae differed between day and night samples. In May 1987, stage I larvae were always more abundant in the upper layer (above 30 m), but there was a distinct shift in the distribution toward the surface at night (Fig. 4A). In May 1988, the average vertical position of stage I and II larvae was similar in the daytime with maximum concentrations in the upper layer (Fig. 4B). At night, the pattern remained the same for stage I larvae, but there was evidence of some upward displacement of stage II larvae (Fig. 4B).

In both years, the centre of mass of stage I and II shrimp larvae during daytime was coincident with the depth of maximum pigment concentration or light attenuation (Spearman partial correlation (with depth of maximum $\Delta\sigma_t$ held constant): $r_s = 0.55$, $P < 0.01$) (Table 1). Taxon-specific centre of mass showed the persistence of stage I and II shrimp larvae in the upper layer along with the larval stages of *P. montagui* and crabs. In the daytime, the larvae were located above the other macrozooplankton taxa and the total zooplankton (>250 μm) biomass (Fig. 5).

During the May 1987 series, deviations from the median depth (21.34 m) of the centre of mass showed that the stage I larvae were significantly deeper (i.e., negative deviations) in the daytime and shallower (i.e., positive deviations) at night (Runs test for dichotomized data: $P < 0.05$) (Fig. 6A). In May 1988, the temporal series of deviations from the median (stage I: 17.6 m, stage II: 13.8 m) of the larval centre of mass revealed no significant differences between day and night position for either stage (Runs test for dichotomized data: $P > 0.05$) (Fig. 6B).

Single classification analysis of variance (ANOVA) was used to determine the relationship between shrimp larval size (i.e., carapace length) and depth. Pairs of strata were combined for the analysis to increase the number of larvae in some strata and to reduce the high variability in sample size among depths (Table 2). In addition, in May 1987, the analysis was performed for daytime and nighttime samples independently. There was a significant effect of depth on stage I larval carapace length in May 1987 (day: $F = 3.66$, $P < 0.05$, df = 3,755; night: $F = 5.62$, $P < 0.01$, df = 3,327) and on stage II larvae only in May 1988 (stage I: $F = 2.58$, $P > 0.05$, df = 2,126; stage II: $F = 4.26$, $P < 0.05$, df = 3,163). For May 1987, an a posteriori test for the comparison of means revealed that stage I shrimp larvae in the upper strata (above 20 m), at night, were significantly larger than larvae in the deeper (>20 m) strata (Studentized maximum modulus (GT2-method) test) (Table 2). In May 1988, stage II shrimp larvae between 10 and 20 m (depth of maximum suspended particle concentration) were significantly

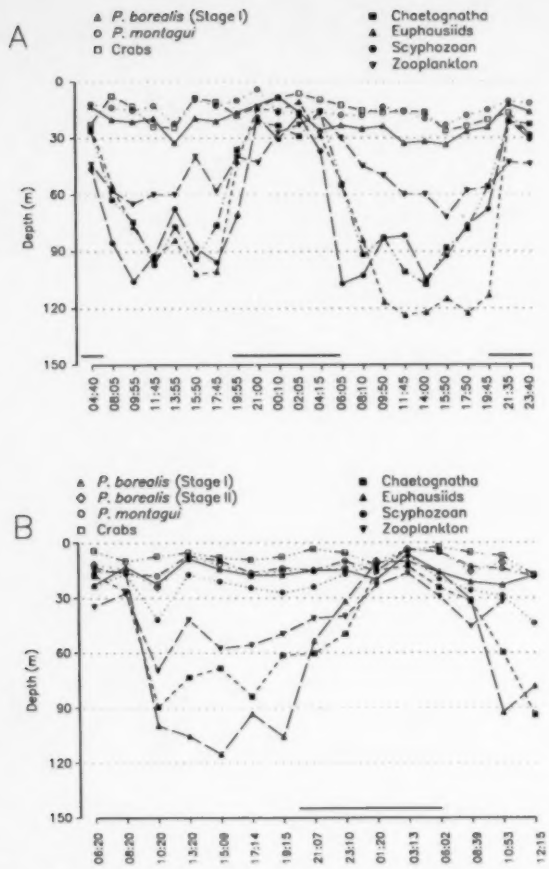

FIG. 5. Centre of mass (m) of all decapod larvae (including *P. borealis*) and macrozooplankton taxa in each set of the (A) May 1987 and (B) May 1988 series. Time of day (EDT) indicates the end of each set, and the horizontal lines represent nighttime.

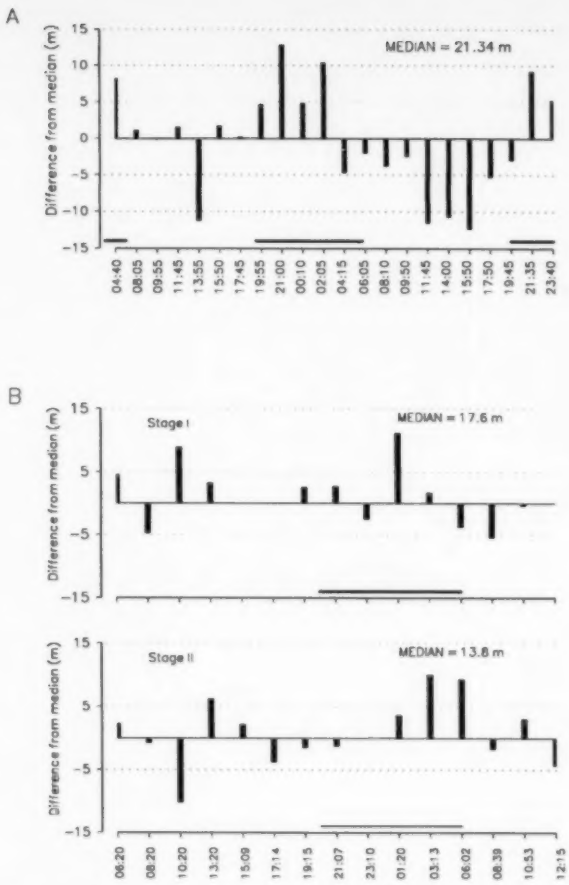

FIG. 6. Time series of the deviations between shrimp larvae centre of mass and the median of the (A) May 1987 and (B) May 1988 series. Time of day (EDT) indicates the end of each BIONESS set, and the horizontal lines represent nighttime.

TABLE 1. Centre of mass (m) of shrimp larvae during day and night sampling periods in May 1987 (N = 16) and May 1988 (N = 11) and depth (m) of maximum pigments concentration (1987) or the light attenuation (a) coefficient maximum (1988). Values for the centre of mass are means ± 1 SD.

Series	Stage	Day	Night	Pigments a (m^{-1})
1987	I	24.9 ± 5.3	13.3 ± 3.2	25
1988	I	17.7 ± 4.5	14.1 ± 5.6	12.5
	II	13.8 ± 5.3	10.7 ± 5.0	

larger than shrimp larvae near the surface (0–10 m) and in the deeper (>20 m) strata (Studentized maximum modulus (GT2-method) test) (Table 2).

Vertical Distribution and Physical Structure of the Water Column

Water temperature and density (σ_t) at the depth of the larval centre of mass were examined to determine the relationship between the physical structure of the water column and the vertical position of the larval stages. The centres of mass of stage I (1987 and 1988) shrimp larvae were correlated with water density (Pearson $r = 0.92$, $P < 0.001$) and temperature (Pearson $r = -0.94$, $P < 0.001$), suggesting that the larvae were not aggregating at specific isopycnals or isotherms (Fig. 7A). However, the daytime vertical position of the larvae was correlated with the depth of the density stratification maximum ($\Delta\sigma_t$) in the water column (Spearman partial correlation (with depth of maximum pigments held constant): $r_s = 0.47$, $P < 0.05$) (Fig. 7B).

Mean and residual current speed and direction (May 1987) were calculated for each depth and for two intervals: (1) a 3-d interval corresponding to the zooplankton sampling series at the site and (2) the entire recording period (i.e., 27 d) (Table 3). Water motion was relatively uniform in speed and direction (northwest) within the water column, but the current was slower and flowed in a different direction close to the bottom (Table 3). The difference in residual and mean current velocities observed for the 27-d period implies a change in direction of the current during the interval.

For an interval of 12 d, corresponding to the duration of the intermoult period (at ~3°C) in stage I shrimp larvae,

TABLE 2. Larval shrimp mean carapace length (CL) (mm) for each group of strata used in the ANOVA test for (A) May 1987 for daytime and nighttime samples and (B) May 1988 for stage I and stage II shrimp larvae (daytime and nighttime samples combined). Boldface values indicate a significantly ($P < 0.05$) larger mean CL among pair of strata (GT2 method test for unequal sample size, Sokal and Rohlf 1981).

(A) 1987

Depth interval (m)	Day		Night	
	Size (N)	CL ± SD	Size (N)	CL ± SD
0 – 10	53	1.12 ± 0.09	**130**	**1.15 ± 0.12**
10 – 20	311	1.1 ± 0.11	**104**	**1.15 ± 0.12**
20 – 50	338	1.08 ± 0.14	69	1.09 ± 0.13
50 – 150	57	1.07 ± 0.11	28	1.1 ± 0.11

(B) 1988

Depth interval (m)	Stage I		Stage II	
	Size (N)	CL ± SD	Size (N)	CL ± SD
0 – 10	—	—	75	1.48 ± 0.2
10 – 20	42	0.89 ± 0.15	**52**	**1.59 ± 0.28**
20 – 50	31	0.87 ± 0.15	32	1.39 ± 0.31
50 – 150	56	0.94 ± 0.14	8	1.56 ± 0.42

the estimated larval net transport (i.e., from the residual current values) was ~50 and ~65 km at 20 and 50 m, respectively.

Discussion

Vertical Distribution and Trophic Implications

Shrimp larvae were about 100 times more abundant at the sampling site in May 1987 than in May 1988. This was probably due in part to the earlier sampling period in 1987, but it may also reflect interannual variability in the horizontal distribution or abundance of shrimp larval groups in the northwest Gulf (Ouellet et al. 1990). However, stage I and II (1988 only) shrimp larvae were concentrated in the upper layer above the cold intermediate layer in both years, despite major differences in the physical structure between years. In addition, the vertical positions of the larvae were coincident with the subsurface maxima of pigments (i.e., chlorophyll *a* and phaeopigments) but different from the zooplankton biomass and other macrozooplankton taxa.

The subsurface chlorophyll *a* maximum may be interpreted as a region of high prey density and a favorable feeding environment for grazers and omnivorous zooplankton (Lasker 1975; Cullen 1982; Napp et al. 1988a). The pigment concentrations were relatively low and the variance high; hence, the results may reflect a change in cell content of chlorophyll *a* with depth (i.e., light adaptation). However, the relationships between the light attenuation maximum and the pigment maximum in 1988 confirmed the presence of higher particle concentrations (probably diatoms) in the vicinity of the pycnocline.

Diatoms are a principal food item for stage I *P. borealis* larvae in the field, although crustacean copepods are also eaten (Stickney and Perkins 1981). Shrimp larval gut contents

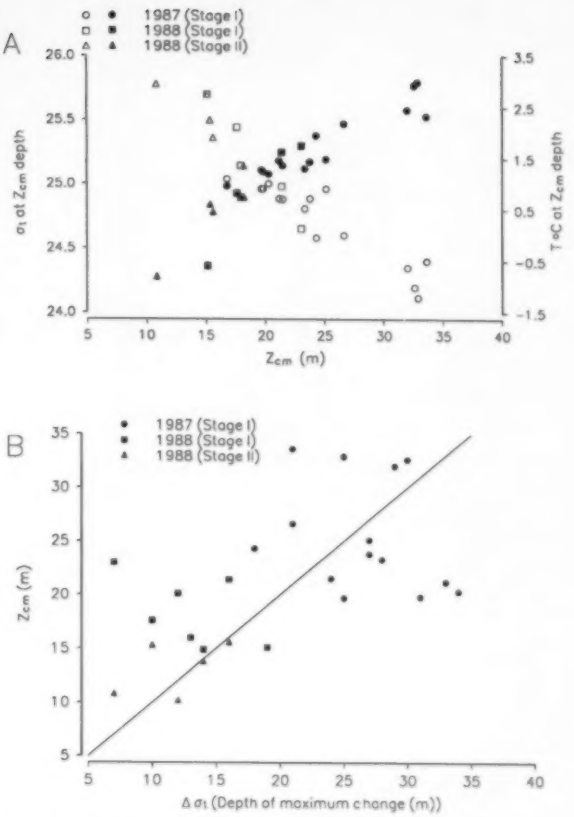

FIG. 7. (A) Water density (σ_t) (solid symbols) and water temperature (open symbols) at the shrimp larvae centre of mass for daytime samples only. (B) Relationship between the shrimp larvae centre of mass (daytime samples only) and the depth of the maximum density (σ_t) difference for both sampling series. The straight line indicates a perfect (correlation of 1) relationship between the depth of the larvae centre of mass and the depth of maximum $\Delta\sigma_t$.

TABLE 3. Residual current speed (cm·s^{-1}) and direction and mean (±1 SD) current speed at each depth in May 1987.

Period	Depth (m)	Residual		Mean speed
		Speed	Direction	
5–7 May (3 d)	20	7.5	349°	7.5 ± 3.5
	50	6.0	331°	6.3 ± 0.7
	95	0.8	53°	1.2 ± 0.9
3–30 May (27 d)	20	4.9	319°	7.6 ± 3.9
	50	6.3	325°	9.0 ± 4.0
	95	3.2	204°	4.3 ± 2.2

were not examined during the sampling; however, the suggestion that the vertical position of the larvae coincident with the suspended particle biomass maximum was advantageous to the larvae is sustained by the larger stage II larvae (i.e., the larvae that had moulted once) found in the upper strata in May 1988. Constant proportions of stage I and II larvae among sampling sets suggest that the same cohort

was sampled during the period and that the stage II larvae sampled were older larvae of the same cohort rather than from a different cohort that had grown in a separate water mass.

Shrimp larvae coexisted with crabs and other decapod larvae in the upper layer. However, the vertical position of shrimp larvae during the day resulted in a spatial segregation of the larvae from the principal macrozooplankton taxa (chaetognaths, scyphozoans, euphausiids, and mesozooplankton grazers) that may represent potential predators or competitors of shrimp larvae. We suggest that the distribution of shrimp larvae in the upper layer could represent an adaptation to trophic pressures within the planktonic community (Fortier and Harris 1989) or an adaptation analogous to the "safe site" hypothesis presented for fish larvae (Frank and Leggett 1982). Although the macrozooplankton taxons migrate toward the surface at night, shrimp larvae were also more dispersed within the upper layer at night, hence reducing their vulnerability to potential predators. The position of shrimp larvae above the permanent pycnocline also served to keep the larvae above the cold (<0°C) intermediate water layer. Larval growth rates, moult frequency, and survival are known to be highly dependent on water temperature (Wienberg 1982; Nunes 1984).

The analysis revealed a nonrandom vertical distribution of the stage I larvae that differed between day and night during 1987. The shortened 1988 series suggested a similar pattern in stage II distribution at night, although differences in the day and night depth distribution were not significant. In addition, the larger stage I shrimp larvae observed in the upper layers (>20 m) at night in May 1987 could be the reflection of differential vertical movement of the larger shrimp larvae. Collectively, these observations suggest a behavioral influence on the vertical distribution. Stage I–IV *P. borealis* larvae were reported to aggregate at about 30 m, below the thermocline in a deep uniform temperature layer in Kachemak Bay (Alaska), and to migrate vertically in a diel cycle (Haynes 1983). These observations indicate depth preferences similar to those observed in our study and also suggest the capability of larval shrimp to maintain their vertical position. Furthermore, the larger partial correlation coefficient for the relationship between the shrimp larvae centre of mass and the subsurface pigment maximum (compare with the partial correlation coefficient between larval centre of mass and strength of the density stratification) indicates the preference of shrimp larvae to maintain a vertical position coincident with potential high food concentrations. However, the relationship between the larval centre of mass and the strength of the density stratification during daytime suggests that passive aggregation of the larvae at the discontinuity layer could also play a role in determining the daytime vertical position.

In a study using a morphometric condition index that represented the nutritional status of larval haddock (*Melanogrammus aeglefinus*), Frank and McRuer (1989) demonstrated that the vertical position (i.e., σ_t at the centre of mass) of the larvae was in part determined by the relative proportion of individuals in poor condition in the cohorts. In addition, Sclafani et al. (1993) argued that larval fish condition and buoyancy can explain most patterns of vertical migrations in the field. We could not provide evidence of differential condition in shrimp larvae among strata based on the morphometric data, although the larger carapace lengths of stage I larvae above 20 m in May 1987 may also be the reflection of better larval condition. Nevertheless, the results suggest that studies of nutritional condition of shrimp larvae in relation to their position in the water column, or to differences in water column structure and feeding environments, would be necessary to further document larval shrimp development and survival in the Gulf waters.

In summary, our analyses suggest that the vertical distribution of stage I and II shrimp larvae may be favorable for enhanced growth within a layer of higher prey concentrations and warmer temperature while maintaining spatial isolation of the larvae from potential macrozooplankton predators or competitors.

Vertical Distribution and Possible Implications for Transport

When averaged over long periods (of the order of weeks) the body of water confined by Anticosti Island, the northwest shore of the Gulf, and the south shore along the Gaspé Peninsula has a cyclonic motion. It is mainly a density-driven circulation, but may be partially wind forced (Koutitonsky and Bugden 1991). The cyclonic eddy is slow (2–5 $cm \cdot s^{-1}$) along the north shore but intensifies in the Gaspé Current (coastal jet current along the Gaspé Peninsula; Fig. 1) where speeds from 50 to 70 $cm \cdot s^{-1}$ have been recorded. Apart from the Gaspé Current region, where the bulk of the current is confined to the top 100 m, the eddy shows no strong amplitude variation with depth (Koutitonsky and Bugden 1991).

The current meter data in May 1987 were consistent with this general circulation pattern. Although the direction of the current at 50 and 20 m was more to the northwest than to the west as anticipated from the cyclonic circulation, this difference is consistent with the bathymetry orientation steering the currents. At the Sept-Îles shore station, the mean daily winds during the same period (May 1987) blew mostly from the west with three noticeable exceptions of easterlies (D. Lefaivre, unpublished data). The depth of the wind-induced current (Ekman depth) would not exceed 35 m on the three days when the wind was blowing from the east. More generally, when the wind was from the west the Ekman depth would not exceed 25 m. These values correspond to the maximum depth where the wind-induced current becomes negligible, so the major effect of the wind will be concentrated in the top 20 m. Moreover, the effect of the stratification of the water column will reduce further this penetration by enhancing the decoupling of the surface waters from the deeper layers (Bugden 1981). Thus, the small variation in the current between 20 and 50 m is probably an effect of the local winds either enhancing the general circulation or reducing it, as is generally the case due to the prevailing westerlies over the sector. Nevertheless, the calculated residual current speeds at 20 and 50 m are within the range of previously published values for the sector. The residual larval transport calculated in the upper layers (~50 to ~65 km, between 20 and 50 m) in May 1987 was of the same order of magnitude as the horizontal scale of stage I larval patches recorded in the northwest Gulf in May 1986 and 1987. The result is consistent with localized and short-duration shrimp larvae emergence in the water column (Ouellet et al. 1990). In addition, the fact that the upper (<50 m) water column was moving uniformly implies limited advantages for shrimp

larvae to control their vertical distribution in terms of advection direction and speed of transport. However, we cannot infer from these data that the conditions were the same within the other sectors of the northern Gulf where larval shrimp aggregations are known to occur (Ouellet et al. 1990).

One exception to the general circulation pattern was the current speed at 95 m (5 m off the bottom) during the three days of the zooplankton sampling. A closer look at the mooring site showed that the current meter was anchored on the southeast side of a small bank (Fig. 1). During that 3-d period, the current flowed toward the north–northwest in the upper layers of the water column, in the direction of the bank. The current was higher than the monthly average whereas in the deep layer the current was strongly reduced and changed direction to follow the contour of the bank. The currents recorded over a longer time interval (27 d) were more to the west as expected from the general circulation in the sector, although the reduction in current speed near the bottom was still observed. It can be shown that the bottom friction in 100 m of water would reduce the current at 95 m to 60% of the value measured at 50 m (Tee et al. 1987). The observed reduction at 95 m, for the period of 27 d, was only slightly greater (50%) than the one expected from bottom friction alone. The difference is interpreted as the effect of the proximity of the bank on the local circulation. The effect was most clearly seen during the 3-d sampling period when the general circulation was toward the bank.

The observation that the bottom currents were affected by the specific topography of the sector illustrates the well-documented feature that water currents tend to follow constant depth contours. The phenomenon can also have a major consequence for the shrimp larvae that emerged close to a bank. Even though our data are too limited to show the long-term change in orientation of the residual current as it flows westward, it is highly probable that a proportion of the larvae will circle around those northern banks. Future studies will investigate whether the larvae circulate long enough to mature and settle close to the banks.

In conclusion, the analysis suggests that water mass circulation in the northwest Gulf of St. Lawrence is favorable to the maintenance of larval shrimp cohorts within the boundaries (200 km west–east × 130 km north–south) of the sector, at least for a period longer than the developmental time for the first pelagic stages. Hence, ecological factors affecting larval survival in the water column are probably responsible for the horizontal (resultant) pattern of abundance distribution of the stage II (and later) shrimp larvae (Ouellet et al. 1990). The next question for further study is to what extent does spatial variability in stratification and water column structure, and the resulting planktonic communities (Kiørboe et al. 1990), affect larval growth and survival within and among the sectors of the northern Gulf of St. Lawrence?

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Elemental Patterns in Red Hind (*Epinephelus guttatus*) Otoliths from Bermuda and Puerto Rico Reflect Growth Rate, Not Temperature

Yvonne Sadovy[1,2]

Fisheries Research Laboratory, P.O. Box 3665, Mayagüez, PR 00708

and Kenneth P. Severin[3]

Department of Geology and Geophysics, Box 755780, University of Alaska Fairbanks, Fairbanks, AK 99775-5780, USA

Sadovy, Y., and K.P. Severin. 1994. Elemental patterns in red hind (*Epinephelus guttatus*) otoliths from Bermuda and Puerto Rico reflect growth rate, not temperature. Can. J. Fish. Aquat. Sci. 51: 133-141.

Sodium, sulfur, calcium, and strontium concentrations were measured (with an electron microprobe) across sectioned wild red hind (*Epinephelus guttatus*) otoliths from Puerto Rico and Bermuda. A single inverse relationship between strontium/calcium (Sr/Ca) ratios and log body growth rate describes the data from both localities. Patterns in Sr/Ca ratios have been used to infer temperature histories of individual fish; our data indicate that there is not a single Sr/Ca–temperature relationship capable of yielding a plausible temperature history across a single otolith, nor is there one that could give reasonable temperature histories for both the Puerto Rico and Bermuda otoliths. Previous findings of Sr/Ca–temperature relationships could be the result of body growth rate being correlated with temperature.

Des chercheurs ont mesuré (au moyen d'une sonde électronique) les concentrations de sodium, de soufre, de calcium et de strontium dans des coupes transversales d'otolithes de mérou couronné sauvage (*Epinephelus guttatus*) de Puerto Rico et des Bermudes. Une relation inverse simple entre les rapports strontium/calcium (Sr/Ca) et le logarithme du taux de croissance corporelle décrit les données recueillies aux deux endroits. Les profils des rapports Sr/Ca ont été utilisés pour établir les antécédents thermiques dans la vie de chaque poisson; d'après les données que nous avons ontenues, il n'existe pas de rapport unique entre Sr/Ca et la température permettant d'établir des antécédents thermiques plausibles à partir de la coupe transversale d'un seul otolithe, ni même un seul rapport qui peut donner des données thermiques raisonnables pour les otolithes de poissons provenant de Puerto Rico et des Bermudes. Des résultats antérieurs sur le rapport entre Sr/Ca et la température pourraient être le résultat d'une corrélation entre le taux de croissance corporelle et la température.

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Optical and chemical patterns in aragonitic otoliths are commonly used to age fish and have also been used to infer external environmental parameters, events, or changes in internal metabolism (Pannella 1980; Casselman 1982; Victor 1982; Brothers 1987; Radtke 1988; Kalish 1989, 1990). In corals and molluscs, strontium levels in inorganically precipitated aragonite are inversely related to temperature (Smith et al. 1979; Schneider and Smith 1982) and this relationship has likewise been suggested for the otoliths of fishes (Radtke and Targett 1984; Radtke 1987, 1989; Townsend et al. 1989). In an earlier study (Sadovy and Severin 1992), we found that strontium/calcium (Sr/Ca) ratios could not be used to infer environmental temperatures for white grunt (*Haemulon plumieri*) (Pisces: Haemulidae) taken from two areas with different temperature regimes, Puerto Rico in the Caribbean and the Carolinas on the east coast of the United States. However, a single relationship could describe Sr/Ca ratios and growth rate, as determined by growth in length, for individuals from both locations, even though von Bertalanffy growth parameters (K and L_∞) (von Bertalanffy 1938) differed markedly between the two areas.

In the present study, we examine the relationships between Sr/Ca ratios, temperature, and somatic growth for two populations of the red hind (*Epinephelus guttatus*) (Pisces: Serranidae). Our aim is to test whether a Sr/Ca – growth rate relationship applies to this species, as it did to the unrelated white grunt, indicating that this relationship might apply more widely in the teleosts. We compared the hypotheses of temperature versus somatic growth determination of Sr/Ca ratios by examining the sagittal otoliths of two populations of wild red hind, one taken from Puerto Rico and the other from Bermuda. As a measure of somatic growth, we used mean annual growth rates in length calculated for each age class from individual growth curves.

Materials and Methods

Fish

Otoliths assessed for strontium and calcium abundance were taken from fish collected from western Puerto Rico,

[1]Order of authorship is alphabetical, no seniority is implied.
[2]Present address: Department of Zoology, University of Hong Kong, Pok Fu Lam Road, Hong Kong.
[3]Author to whom correspondence should be addressed.

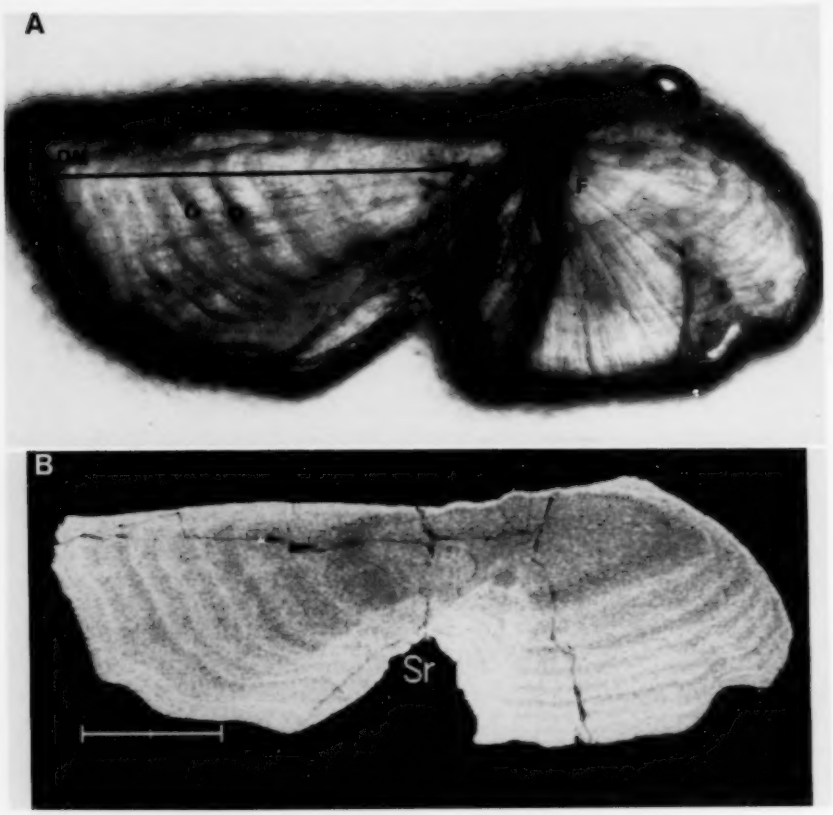

FIG. 1. Light photograph and X-ray map of an otolith section from red hind from Puerto Rico. Scale bar = 1 mm. Pixels are 10 × 10 μm. (A) Viewed under transmitted light showing focus (F), otolith dorsal margin (DM), and opaque zones (O); the line indicates the position of the microprobe traverse. (B) X-ray map; the bright areas indicate the highest concentrations of strontium.

by hook-and-line and fish trap, between June 17 and 23, 1988. Red hind from Puerto Rico selected for the present study measured between 201 and 314 mm fork length (FL) and were aged between 1 and 6 yr (N = 10). Otoliths from Bermuda were obtained from fish collected by hook-and-line and fish trap between August 6, 1972, and May 12, 1974 (Burnett-Herkes 1975). Fish from Bermuda measured 395–425 mm FL and were aged 7 yr (N = 4).

Otoliths for quantitative analyses were selected on the basis of their optical legibility following sectioning and to ensure inclusion of a wide size and age range of fish. The otoliths had initially been collected for age and growth work according to which growth parameters were similar for both populations (Burnett-Herkes 1975; Sadovy et al. 1992).

Temperature

Temperature data from surface waters and at depth are available from both Puerto Rico and Bermuda. Those for Puerto Rico indicate a range of 25–30°C at 2 m depth (Department of Marine Sciences, University of Puerto Rico) and 25–29°C at 18 m depth (P.L. Colin, Chuuk Atoll Research Laboratory, P.O. Box 70, Weno, Chuuk State, Federated States of Micronesia, 96942, personal communication). For Bermuda, the annual temperature range is 17–28°C for surface waters and 17–27°C at 25 m depth (Burnett-Herkes 1975).

Growth Rate Determination

To calculate growth rates from otoliths, sagittae were removed, washed, sectioned dorsoventrally to 0.36–0.43 mm, and mounted on glass slides. Size-at-age for each fish was determined using a back-calculation formula that allowed estimation of body length at the time of initiation of the formation of each opaque zone appearing in sample otoliths, i.e., at the proximal margin of each opaque zone along a scan line running from the focus to the dorsal margin (Fig. 1 and 2). Using the calculated size-at-age data, growth curves were constructed for each individual. The mean annual growth rate at each opaque zone was determined from the growth curves by calculating the tangent to the curve at each opaque zone. These calculated growth rates provided a single estimate of mean annual growth rate (millimetres per year) for each individual at each opaque zone which could be associated with Sr/Ca ratios measured within the corresponding opaque zone (arrows, Fig. 3 and 4).

The Lee proportional back-calculation formula was used

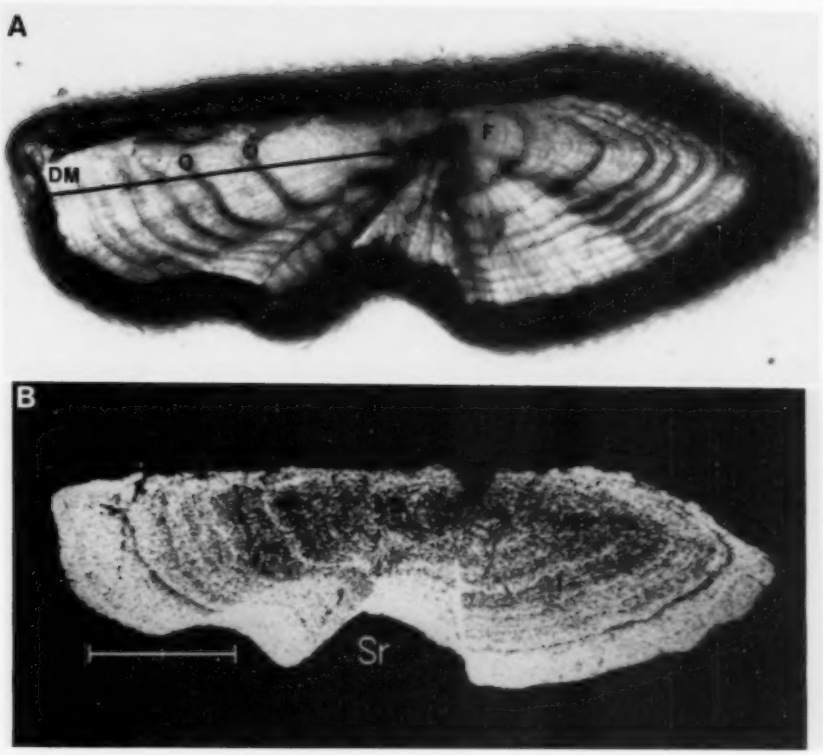

FIG. 2. Light photograph and X-ray map of an otolith section from red hind from Bermuda. Scale bar = 1 mm. Pixels are 10 × 10 μm. (A) Viewed under transmitted light showing focus (F), otolith dorsal margin (DM), and opaque zones (O); the line indicates the position of the microprobe traverse. (B) X-ray map; the bright areas indicate the highest concentrations of strontium.

for back-calculation of length-at-age (Carlander 1981). This equation requires knowledge of the relationship between otolith radius (OR) and FL in otoliths taken at the same time and location as individuals for which individual growth curves are calculated. For details of otolith preparation and analysis, see Sadovy et al. (1992). For Puerto Rico the FL/OR relationship was (Sadovy et al. 1992)

$$FL = 33.218 + 3.0743\ OR;\ N = 624;\ r^2 = 0.76$$

and for Bermuda the relationship was

$$FL = 64.43 + 2.95\ OR;\ N = 44;\ r^2 = 0.79$$

where FL is in millimetres and OR is in micrometre units (32 units = 1 mm).

Growth parameters for the populations from the two locations are similar as described by the von Bertalanffy growth function (von Bertalanffy 1938). For Puerto Rico, L_∞ (asymptotic length) = 515 mm FL and K (Brody growth coefficient, Ricker 1975) = 0.101 (Sadovy et al. 1992), as determined by otoliths. For Bermuda, L_∞ = 505 mm FL and K = 0.180 (Burnett-Herkes 1975) as determined by length–frequency data corroborated by otolith ring counts.

Otolith band pairs (one opaque + one translucent zone as viewed under transmitted light) 1–10 have been validated as annual for fish from Puerto Rico by marginal increment analysis and also in a field study using injected oxytetracycline as a time marker (Sadovy et al. 1992). The temporal nature of the band pairs has not been validated for Bermuda but is assumed to be the same as for Puerto Rico.

Because of problems inherent in back-calculation manipulations (Campana 1990), the relationship between Sr/Ca and age, which is independent of otolith measurements and back-calculation, was also determined. Analyses were not made by sex because the red hind is a protogynous hermaphrodite with many individuals functioning as both female and male in their lifetime: sexual maturation occurs between 2 and 3 yr (Sadovy et al. 1992).

Microprobe Analyses

Sagittal otoliths were sectioned transversely (dorsoventral) with a slow-speed saw. Sections were then mounted on glass slides with thermo-epoxy (Petropoxy 154, Palouse Petro Products, Palouse, Wash., USA), ground on a diamond lap wheel until the focus was exposed, and then polished flat with 0.05-μm alumina on silk. All samples were coated with approximately 25 nm of carbon before examination with the Cameca SX-50 microprobe at the Department of Geology, University of Puerto Rico, Mayagüez (one energy dispersive and three wavelength dispersive spectrometers). Investigations of wavelength spectral scans revealed no elements (atomic number >10) other than sodium, sulfur, calcium, and strontium in enough abundance (greater than about 0.1 weight %) to be analyzed quantitatively.

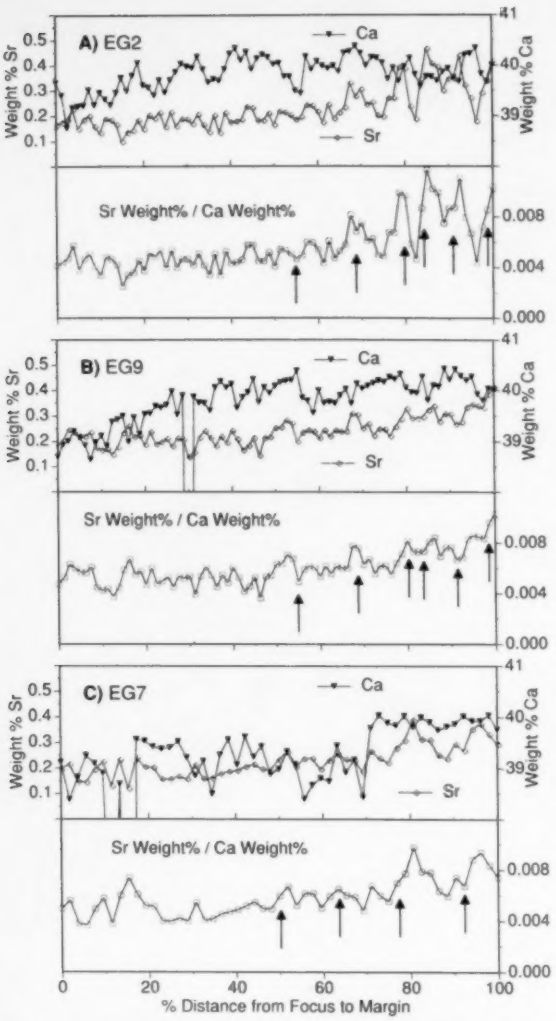

FIG. 3. Elemental concentrations across sectioned otoliths of Puerto Rico fish. Arrows indicate points at initiation of opaque zones, i.e., proximal margins, and associated Sr/Ca values used in the analyses. (A) EG2, caught June 23, 1988, FL = 277 mm, male, 6 yr old; (B) EG9, June 23, 1988, FL = 305 mm, male, 6 yr old; (C) EG7, June 23, 1988, FL = 278 mm, sexually transitional, 4 yr old.

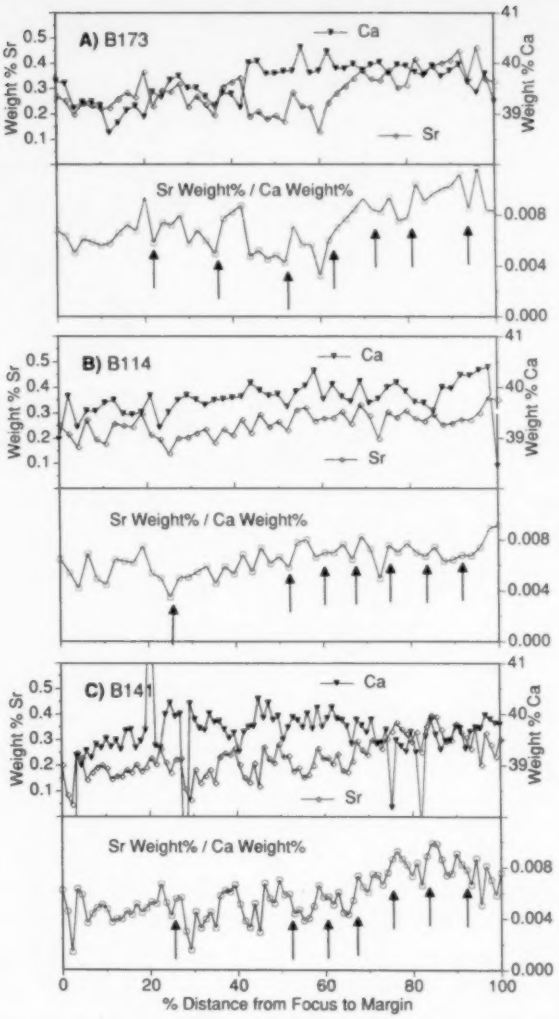

FIG. 4. Elemental concentrations across sectioned otoliths of Bermuda fish. Arrows indicate points at initiation of opaque zones, i.e., proximal margins, and associated Sr/Ca values used in the analyses. (A) B173, caught May 6, 1973, FL = 345 mm, female, 7 yr old; (B) B114, August 6, 1972, FL = 295 mm, sex unknown, 7 yr old; (C) B141, October 10, 1972, FL = 336 mm, sex unknown, 7 yr old.

Patterns in strontium and calcium abundance were measured along a traverse from the otolith focus to the otolith margin (Fig. 1A). Analytical conditions and precision for the calcium and strontium measurements reported here are summarized in Table 1. Digital X-ray maps of sectioned otoliths were produced on the Cameca SX-50 at the Laboratory for Microbeam Analysis, University of Alaska Fairbanks (one energy dispersive and four wavelength dispersive spectrometers). Detailed discussion of the acquisition and processing of X-ray maps may be found in Goldstein et al. (1992).

Measured variability in trace element abundance across a single otolith results from several factors. Some arise because of errors inherent in the microprobe's ability to detect low levels of trace elements, particularly when analyzing carbonates. Carbonates are sensitive to thermal decomposition caused during the electron beam/sample interaction (Smith 1986), and the usual techniques of increased beam current or increased counting times cannot be applied. Gunn et al. (1992) discussed various electron microprobe operating parameters as they pertain to otolith analysis.

We chose to use Sr/Ca ratios to compare with growth rate data because electron microprobe analyses of otoliths for strontium and calcium (and other minor cations) do not directly yield otolin concentrations (the organic matrix of otoliths, see Morales-Nin 1987 for summary). Otolin concentrations can only be estimated by assuming that the measured cations are contained in the aragonite and stoichio-

TABLE 1. Analytical conditions, standards, and relative errors due to counting. Data were collected with a 15-kV, 2-nA beam current electron beam rastered across a 20 × 35 μm area once every 6 s. This was the highest beam current and smallest area that did not produce measurable thermal decomposition of the aragonitic otoliths (Smith 1986).

Element and standard	Weight %	Peak counts	Background counts	Net counts	σ_{net}[a]	Relative precision, weight % (1 σ)[b]
Calcium[c]						
Calcite (USNM 13621) 40.09						
weight % Ca	38.382	84 234	275	80 778	285.2 counts 0.35% of net	0.135
	40.033	81 053	275	83 959	290.7 counts 0.35% of net	0.139
Strontium[d]						
Strontianite (USNM R10065) 55.20						
weight % Sr	0.156	446	258	188	26.5 counts 14.11% of net	0.022
	0.389	687	221	466	30.1 counts 6.47% of net	0.025

[a]Standard deviation due to counting statistics (σ_{net}) is calculated from $\sigma_{net} = (\sigma^2_{peak} + \sigma^2_{background})^{1/2}$. Because σ^2_{peak} or $\sigma^2_{background}$ = the number of counts recorded for the peak or background, $\sigma_{net} = (N_{peak} + N_{background})^{1/2}$.

[b]σ_{net} can be divided into the net number of counts to obtain a relative standard deviation. Data (from a traverse across EG7, June 23) for high and low concentrations are presented because relative precision is a function of elemental concentration. See Williams (1987) for more discussion of precision and accuracy of X-ray analyses.

[c]Calcium *Kα* X-rays were measured with a Kevex 8000 energy dispersive spectrometer. X-rays were collected for 100 s (live time); the peak was deconvoluted and quantified with Kevex-Quantex software.

[d]Strontium *Lα* X-rays were measured with a wavelength dispersive spectrometer (TAP crystal). X-rays were counted for 100 s at the emission peak, and the background was determined for a total of 100 s, 50 s on either side of the peak.

metrically estimating the amount of otolin. Implicit in this method is the assumption that the otolin does not contain significant amounts of cations. Under this assumption, Sr/Ca ratios are independent of the otolin/aragonite ratio and are measures of the relative amounts of strontium and calcium in the aragonite. If absolute strontium abundances were used, then it would not be possible to differentiate between analyses that yielded, for example, 1% strontium, 35% calcium, 5% otolin and 1% strontium, 40% calcium, 0% otolin.

Spatial resolution of trace element abundances across an otolith remains constant, but temporal resolution does not because otoliths do not grow at a constant rate. In the case of red hind, the analyzed area (20 × 35 μm) spans about a 2-wk time period in the juvenile portion of an otolith and individual analyses are separated by approximately 1-mo intervals. In the adult portion of an otolith, because of slower otolith growth, each analyzed area covers about 1 mo and analyses are separated by approximately 2 mo. Thus, variability detected in the proximal, younger portions of otolith scans reflects a shorter time span than variability in more distal regions; the two should be compared with caution. Short-term growth rate fluctuations below the level of resolution of individual microprobe measurements could obscure Sr/Ca – growth relationships.

Results

General Distribution of Elements

The patterns of elemental abundance from the focus to the dorsal margin of sectioned otoliths of red hind from both locations approximated the optical banding pattern as viewed under transmitted light (compare Fig. 1A and 1B, 2A and 2B). Visual inspection indicated that concordance between optical bands and patterns of elemental abundance was closer in some otoliths (Fig. 3A, 3C, and 4A) than in others (Fig. 3B, 4B, and 4C). Strontium maxima and calcium minima coincided approximately with opaque zones (Fig. 3 and 4; arrows indicate the proximal border of successive opaque zones).

Relationship between Sr/Ca Ratios and Temperature

Several studies have suggested an inverse relationship between Sr/Ca ratios and temperature in fish otoliths. If this type of relationship exists for the red hind, then Sr/Ca maxima should represent times of temperature minima and vice versa. Interpreting our data under this hypothesis, the Sr/Ca ratios across otoliths of fish from Puerto Rico (Fig. 3 and 5) suggest that the fish spent the early portions of their lives (until about 1 yr old) in relatively warm water (compared with the rest of the life cycle) and then moved between, or encountered in their areas of residence, cycles of cold and warm water, with a net shift into cooler water with increasing age. While it is true that red hind juveniles generally settle inshore and move progressively offshore as they grow, large individuals are frequently found inshore and small individuals occur in deeper water (Burnett-Herkes 1975; Y. Sadovy, personal observation).

A similar interpretation is valid for Bermuda fish (Fig. 4), with the exception that they did not experience the same annual temperature extremes during their adult lives as the Puerto Rico fish. Furthermore, because the range of Sr/Ca ratios in otolith sections is similar in both locations (0.002–0.010), we would conclude that the annual temperature range in both locations is similar. Instead, the tem-

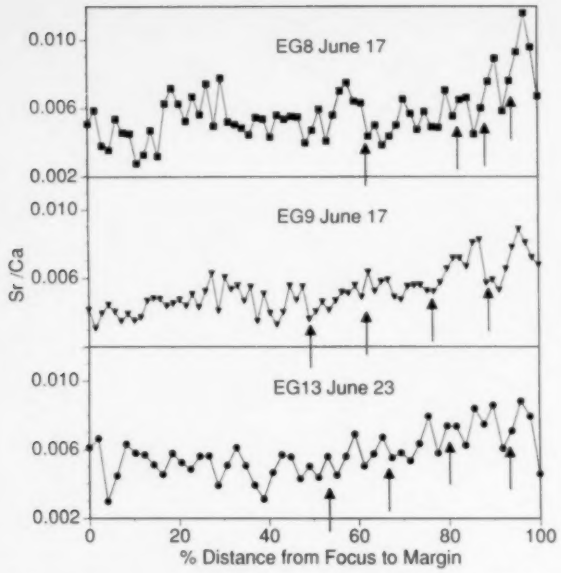

FIG. 5. Comparison of Sr/Ca ratios across EG8 (June 17, FL = 225 mm), EG9 (June 17, FL = 261 mm), and EG13 (June 23, FL = 235 mm), all 4-yr-old females taken in 1988. Although these individuals were caught within 1 wk of each other in the same location, the patterns of the Sr/Ca ratios differ.

perature range for the Puerto Rico fish is about 5°C and the range for the Bermuda fish is twice that, about 10°C.

A comparison of Sr/Ca ratios across the otoliths of similarly aged (4 yr old) individuals in Puerto Rico, collected from the same area at the same time, showed markedly different patterns (Fig. 5). If the Sr/Ca ratios were controlled by a single physical factor, such as temperature, then the Sr/Ca ratios in all these individuals should be similar. The fact that they differ indicates either that individual life-history temperature profiles vary substantially, which seems unlikely, or that temperature was not the principle factor determining Sr/Ca ratios.

Sr/Ca ratios at otolith margins showed no consistent pattern in either increase or decrease of Sr/Ca with season of capture. This observation was particularly striking in otoliths of Puerto Rico fish. First, Sr/Ca ratios at the otolith margins spanned much of the range seen across all the otoliths (0.004–0.010). Second, Fig. 3A and 3B show Sr/Ca ratios increasing at the margins of two fish captured on June 23, 1988, while in Fig. 3C and 5 they were decreasing at the margins of four fish caught at the same location between June 17 and 23, 1988. Again, based on the "temperature" hypothesis, we would conclude that two of these animals were experiencing decreasing temperatures at the time of capture, while four others were experiencing increasing temperatures. This interpretation is unlikely given that all fish were caught at the same location within 1 wk of each other.

Finally, if this hypothesized relationship holds, then Sr/Ca maxima should occur at the times of lowest temperature. However, despite some variability, strontium maxima were generally associated with opaque zones. In Puerto Rico, opaque zones in red hind otoliths are formed in the spring and summer (Sadovy et al. 1992), when water temperatures are either rising or are at their annual maximum (Sadovy and Severin 1992). Sr/Ca maxima were thus more directly associated with high or rising, rather than low, environmental temperatures. While it is, perhaps, tempting to invoke some sort of time lag to make the Sr/Ca maxima match temperature minima, any such lag requires the abandonment of the inorganic precipitation model for this system. Moreover, opaque zone formation tends to occur earlier in the year in younger than in older fish (Sadovy et al. 1992). A similar intraspecific temporal variation in opaque zone formation has been reported in other species (Moe 1969; Casselman 1974). Such temporal variation is inconsistent with a single principal environmental variable being the major causative agent of opaque zone formation and associated high Sr/Ca ratios in red hind. Moe (1969) proposed that the different timing of annulus formation in older age groups in red grouper (*Epinephelus morio*) probably reflects a slower metabolic rate and a shorter annual growth period compared with younger age groups.

There does not appear to be a single, simple relationship consistent with an inverse Sr/Ca ratio – temperature correlation in the red hind, either for individuals from two different geographic locations or within a single location.

Relationship between Sr/Ca Ratios and Age

An ANCOVA showed that location ($F_{1,68} = 14.44$, $p = 0.0003$, $N = 71$) and age, as estimated by opaque zones ($F_{1,68} = 47.07$, $p = 0.0001$, $N = 71$), are significant predictors of Sr/Ca ratios and that the regressions between age and Sr/Ca values at the two localities are indistinguishable ($F_{1,67} = 0.59$, $p = 0.4437$, $N = 71$). The significance of location in predicting Sr/Ca ratios is probably due to the different-aged samples from the two localities, as indicated by location being not significant ($F_{1,68} = 1.19$, $p = 0.2802$, $N = 71$) when the age–location interaction term is included in the model. The regression of age and Sr/Ca ratios for the combined localities is

$$\text{Sr/Ca} = -0.000495 \text{ age} + 0.005101;\ F_{1,69} = 30.522;\ p = 0.0001;\ N = 55;\ r^2 = 0.30.$$

Relationship between Sr/Ca Ratios and Growth Rate

Because of difficulties in the optical resolution of growth zones near the otolith margin of older fish, and in distinguishing the proximal margin of the innermost zone, only growth rates from opaque zones distal to the innermost zone and growth rates greater than 10 mm/band pair annually were used in the analyses. Sr/Ca ratios at each opaque zone were plotted against the back-calculated average annual growth rate for the age class designated by that zone. Inspection of the data suggested that relationships between growth rates and Sr/Ca ratios were best described by log-transforming the growth rate data.

The Sr/Ca values used were those that were optically determined to be at the proximal edge of each opaque zone (values indicated by arrows in Fig. 3, 4 and 5). The regression of log growth rate and Sr/Ca ratios was significant for fish from both Puerto Rico ($F_{1,30} = 9.74$; $p = 0.0040$; $N = 32$; $r^2 = 0.22$) and Bermuda ($F_{1,21} = 6.85$; $p = 0.0161$; $N = 23$; $r^2 = 0.21$) fish. An ANCOVA showed that location was not significant in predicting Sr/Ca ratios ($F_{1,21} = 1.98$; $p = 0.166$), that log growth rate was significant ($F_{1,52} = 16.78$; $p =$

0.0001), and that the regressions between Sr/Ca ratios and log growth rate at the two locations (interaction) were not distinguishable ($F_{1,51} = 0.10$; $p = 0.751$). The regression of log growth rate and Sr/Ca ratios for the combined localities is

$$\text{Sr/Ca} = -0.001856 \ln(\text{GR}) + 0.012933;\ F_{1,53} = 16.485;$$
$$p = 0.0001;\ N = 55;\ r^2 = 0.24.$$

Figure 6 shows the relationships between Sr/Ca and growth rate in fish from both locations separately and then combined. The three regressions do not differ substantially, and any one of them could be used to describe the data, again suggesting that a single relationship exists between growth rate and Sr/Ca ratios for fish from geographically separate locations.

Discussion

The patterns of strontium abundance and Sr/Ca ratios across sectioned otoliths of wild red hind from Bermuda and Puerto Rico do not support the hypothesis that a simple inverse relationship exists between Sr/Ca ratios and temperature. On the other hand, similar significant relationships between log body growth rate and Sr/Ca ratios were found for red hind from both Puerto Rico and Bermuda. The significant relationship between Sr/Ca ratio and age for both Puerto Rico and Bermuda is consistent with a Sr/Ca ratio – growth rate hypothesis and inconsistent with one invoking temperature because age and growth rate are related, while age and temperature are not. A direct Sr/Ca–age relationship would not account for results of other workers, however, nor for the interindividual variabilities in Sr/Ca ratios-at-age described in this study.

Although salinity has been implicated in affecting the Sr/Ca ratios in otoliths (Radtke et al. 1988), the red hind is a marine species characteristically found in offshore and reef habitats. Because red hind spend their entire life in well-mixed marine waters, there is no reason to expect that the populations in Puerto Rico and Bermuda experience different salinities or seawater strontium concentrations during their lives (Culkin and Cox 1966; Brass and Turekian 1972).

A Sr/Ca – growth rate relationship is a consistent alternative explanation for all other published experimental results on Sr/Ca ratios in fish otoliths for which a temperature relationship has been proposed, with the exception of one, the Hawaiian snapper (*Pristipomoides filamentosus*) (Radtke 1987), where Sr/Ca values decrease during the life of the fish. Kalish (1989) reported a significant relationship between Sr/Ca and age in blue grenadier (*Macruronus novaezelandiae*) and proposed that seasonal variations in otolith chemistry in both wild blue grenadier and Australian salmon (*Arripis trutta*) are partly due to seasonal changes in growth rates and/or reproductive investment. He found no Sr/Ca–temperature relationship for either species. In the bearded rock cod (*Pseudophycis barbatus*), Kalish (1991) found significant seasonal variation in otolith Sr/Ca ratios and was able to explain 52% of the Sr/Ca variability in male and female otoliths by considering six factors, including fish weight and gonad weight, but not temperature.

While gross seasonal changes in growth rate over the annual cycle probably account for a significant proportion of the variation in Sr/Ca levels across otolith sections for Puerto Rico fish, irregularities and interindividual variations in the pattern of the microprobe traverses clearly show that other

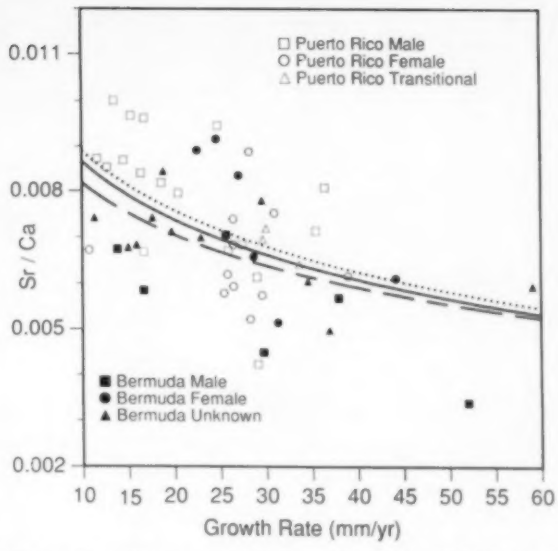

FIG. 6. Growth rate versus Sr/Ca ratios. The solid line is the regression based on data from Puerto Rico and Bermuda fish combined, the dotted line is based on data from Puerto Rico fish only, and the broken line is based on data from Bermuda fish only. The figured regressions describe the data equally well and suggest a significant relationship between log growth rate and Sr/Ca ratios.

factors are also involved. These factors include both errors associated with the measurement of Sr/Ca ratios (see section on Microprobe Analyses) and growth rates and irregular events that also impact growth. For example, Cailliet and Radtke (1987) attributed irregular fluctuations of calcium and phosphorus in the centra of gray reef sharks to life-history events such as temporarily decreased food supply, temperature changes, metabolic pauses, or injury-related phenomena.

The high variability of growth rate-at-age between individuals from a single location indicates that growth rate is influenced by many factors. Moreover, because data were analyzed for growth-in-length, rather than growth-in-weight, as an indicator of somatic growth, weight changes in larger fish are likely to be grossly underrepresented and may be considerable due to weight fluctuations caused by variations in food availability or reproductive condition (Moreau 1987). The most likely factors to influence growth rate in fish are food supply or rate of consumption, environmental temperature, ambient oxygen, salinity, reproductive activity, migrations, genetics, and age (Weatherley and Gill 1987). Reproductive activity is not likely to be a major cause of Sr/Ca variability in the red hind because there are no noticeable differences in Sr/Ca ratios for individuals in the male, versus the female, phase despite the fact that ripe ovaries attain four to five times the size of ripe testes. Moreover, despite the fact that the annual reproductive period is brief, lasting 2 mo at most, there is no discernible signal in Sr/Ca ratios that would suggest a direct correlation with such a well-defined period of spawning activity (Y. Sadovy, A. Rosario, and A. Román, unpublished data).

The results of the analyses of red hind otoliths from two geographic locations are similar to those for the white grunt

from Puerto Rico and the Carolinas (Sadovy and Severin 1992). The gradual rise and increasing variability in Sr/Ca ratios across otolith sections is similar to, although somewhat less extreme than, that observed in the white grunt in Puerto Rico, a fish that characteristically occupies a lesser maximum depth than the red hind (Sadovy and Severin 1992). In both studies, the Sr/Ca–temperature hypothesis was rejected, and a similarly significant relationship was found between Sr/Ca ratios and growth, with considerable variability still unexplained. For both species the overall form of the relationship for both geographic areas was similar. In Puerto Rico, Sr/Ca ratios in older white grunt showed markedly similar trends to those in the red hind but exhibited a more regular and marked oscillation than was observed for the red hind in this study, suggesting species-specific effects. For both species the elemental distribution patterns from the more northern locations were somewhat more irregular than for Puerto Rico. The reason(s) for these intra- and interspecific differences is not known.

If somatic growth proves to be a principal cause of Sr/Ca variation across fish otoliths, analysis of otolith Sr/Ca holds potential for understanding many aspects of life history that are virtually inaccessible using currently available methods. The possible role of the various factors likely to influence growth rate and, hence, Sr/Ca levels, would need to be examined by controlled laboratory experiments for all sizes, ages, seasons, and reproductive conditions to understand the extent of their effects on growth rate variation. It may be possible to estimate otolith Sr/Ca directly from living fish, as the Sr/Ca content of the saccular endolymph is reported to be linearly correlated with otolith Sr/Ca ratios (Kalish 1989). The effect of selecting different radii for traverses within otoliths should be evaluated (Gauldie and Nelson 1990), and any time lag involved between changes in growth rates and changes of otolith Sr/Ca ratios must be understood before these become the indicators they promise to be. Different measures of somatic growth would need to be evaluated.

Despite the possible value of Sr/Ca ratios in unraveling various aspects of life history, caution is needed in interpreting Sr/Ca ratios because of the many factors that may influence them (Kalish 1989, 1991). Indeed, since growth rate itself is often likely to be strongly temperature influenced, deconvolution of temperature and growth effects is particularly critical. However, if properly and carefully applied, Sr/Ca information eventually could become a valuable tool for refining our knowledge of growth history.

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Observations of Adult Atlantic Cod (*Gadus morhua*) Overwintering in Nearshore Waters of Trinity Bay, Newfoundland

J.S. Wroblewski, Wade L. Bailey, and Kristine A. Howse

Fisheries Oceanography Group, Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, NF A1B 3X7, Canada

Wroblewski, J.S., W.L. Bailey, and K.A. Howse. 1994. Observations of adult Atlantic cod (*Gadus morhua*) overwintering in nearshore waters of Trinity Bay, Newfoundland. Can. J. Fish. Aquat. Sci. 51: 142–150.

In the Random Island region of Trinity Bay, Newfoundland, individual adult Atlantic cod (*Gadus morhua*) with surgically implanted sonic transmitters were repeatedly relocated during the winter of 1990–91. Cod remained near shore, where seawater temperatures were as low as −1.5°C. These fish did not move in the fall to offshore continental shelf waters as do most northern cod, nor did they move into the deeper waters of Trinity Bay that were slightly warmer than those in the nearshore zone. Of 12 cod released with transmitters in the fall and early winter, two were caught by local inshore fishermen the following spring, providing evidence that adult cod that overwinter nearshore become available to the spring inshore fishery. Another three were caught within a year of release. One fish was hooked in Fortune Bay on the southern coast of Newfoundland, having traveled a minimum distance of 305 nautical miles. These results demonstrate that northern cod can survive the surgical implantation of transmitters for at least a year and that this method is a valid technique for studying the behavior of northern cod. The main limitation to our sonic tracking was the relatively short range of signal reception (<1 nautical mile).

Dans la région de l'île Random dans la baie Trinité (Terre-Neuve), chaque morue franche (*Gadus morhua*) adulte proteuse d'un radio-émetteur sonique implanté par chirurgie a été relocalisée à maintes reprises au cours de l'hiver 1990–1991. Les morues demeuraient près de la côté où la température de l'eau de mer atteignait à peine −1,5 °C. À l'automne, ces poissons ne migraient ni dans les eaux de la plate-forme continentale comme le font la plupart des morues du nord ni dans les eaux plus profondes de la baie Trinité qui étaient un peu plus chaudes que celles de la zone littorale. Sur les douze morues porteuses d'émetteur relâchées à l'automne et au début de l'hiver, deux ont été capturées par des pêcheurs côtiers le printemps suivant, ce qui prouve que la morue adulte qui passe l'hiver dans la zone précôtière est vulnérable à la pêche côtière printanière. Trois autres morues ont été capturées moins d'un an après avoir été relâchées. Un poisson a été pris à l'hameçon dans la baie Fortune sur la côte sud de Terre-Neuve, après avoir franchi au moins 305 milles marins. Ces résultats montrent que la morue du nord peut survivre à une implantation chirurgicale d'émetteur pendant au moins un an, et que cette méthode est une technique valable pour étudier le comportement de la morue du nord. La principale limite à notre radio-pistage était la portée relativement courte de réception des signaux (< 1 mille marin).

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The seasonal migration pattern of Atlantic cod (*Gadus morhua*) living off the northeast coast of Newfoundland shows that fish migrate inshore in summer and offshore in the fall to overwinter and spawn over the continental shelf (Templeman 1979; Lear and Green 1984). The nearshore zone is considered the summer feeding grounds for adults and the nursery ground for developing juveniles that eventually move into deeper offshore waters with increasing age (Templeman and Fleming 1963; Lear and Green 1984). This migration behavior model describes the "typical" movements of the major components of the northern cod stock. However, it has long been suspected that some cod remain in the larger bays such as Trinity Bay and Bonavista Bay, perhaps never leaving them (Thompson 1943).

Cod that move offshore onto the northeast Newfoundland continental shelf are typically found overwintering in waters of 0–3°C (Templeman and Fleming 1963; Templeman and May 1965). During the summer, cod along the coast are most frequently located at temperatures between 0 and 5°C (Lear et al. 1986; Rose and Leggett 1988). In winter when nearshore waters become chilled below −1°C, it is believed that adult cod move to deeper, warmer waters (Templeman and Fleming 1956). Deep bays such as Trinity Bay have comparatively warm bottom waters in which the local cod might spend the winter (Thompson 1943).

In a laboratory study, Goddard et al. (1992) found that juvenile cod had significantly higher plasma antifreeze levels than adults during the winter (January–March), suggesting that small cod are capable of surviving harsher winter conditions than adults. Goddard et al. (1992) proposed that antifreeze production may have a bearing on habitat selection and overwintering behavior of northern cod at different stages of development.

The intent of our field study was to observe the behavioral response of cod in Trinity Bay to winter cooling of nearshore waters. We hypothesized that adult cod would move offshore, or at least into the deeper parts of the bay as the season progressed.

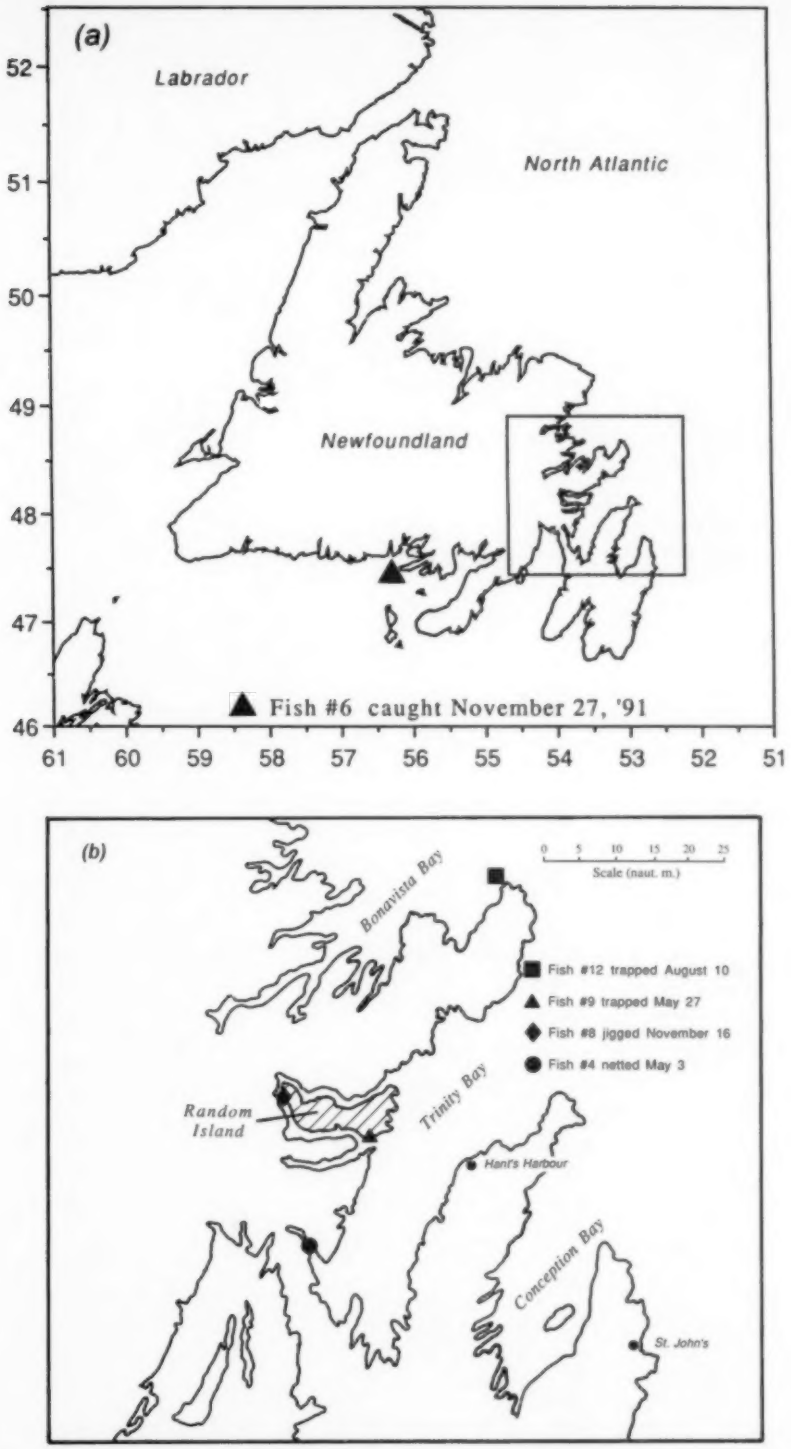

FIG. 1. Sites of recapture of sonically tagged cod by fishermen. (a) Location (triangle) where fish 6 was caught on November 27, 1991; (b) locations where fish 4, 8, 9, and 12 were caught by fishermen in 1991. Study area is the Random Island region of Trinity Bay.

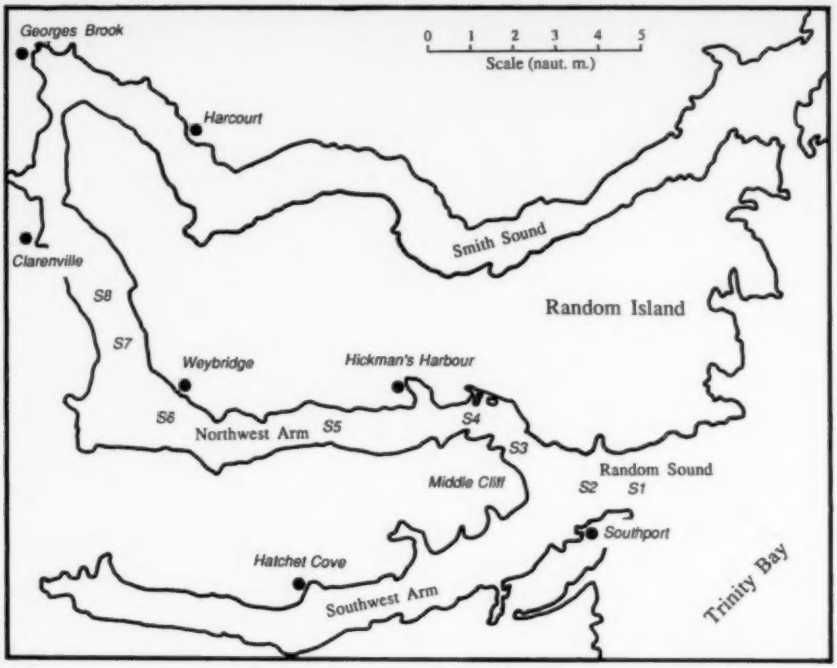

FIG. 2. Location of geographical names mentioned in the text and stations S1–S8 for the temperature survey shown in Fig. 3.

Materials and Methods

Tag–recapture studies of northern cod have shown that movements of individual cod vary widely from a few to hundreds of nautical miles distance, in directions along the coastline or between the coast and the offshore banks (Thompson 1943; Templeman 1979; Lear 1984). However, neither tag–recapture studies nor presence–absence sampling by experimental fishing (e.g., Templeman and Fleming 1956, 1963) provide information on movement of individual fish beyond the time of encounter.

Sonic tagging (Hawkins and Urguhart 1983; Arnold and Metcalfe 1989; Clark and Green 1990) allows one to track the movements of individual fish continuously and to acoustically relocate a fish. However, the number of fish that can be observed is small relative to numbers involved in tag–recapture studies. Sonic tagging allowed us to obtain a series of observations on individual northern cod during the period of coldest ocean temperatures when there is little commercial fishing and therefore limited information from tag–recapture studies.

Choice of Study Area

The Random Island region of Trinity Bay (Fig. 1) was chosen as the study site because there was an active inshore cod fishery in the area. The local geography also facilitates tracking. The narrow basins of Smith Sound, Northwest Arm, and Southwest Arm are approximately 2 nautical miles in width (Fig. 2). The shoreline was often within the range of tracking instrumentation located in the centre of the channel. Therefore the research vessel needed only to move up and down the sounds to search in all directions.

Sonic Tagging

Twelve cod were tagged with pinger transmitters and released into the waters of the Random Island region during the late fall and early winter of 1990–91 (Table 1). On November 28, four cod were caught on longline in Smith Sound off Harcourt (Fig. 2), measured for length and weight, and then surgically implanted with transmitters and released. Water temperature at the site was 2°C from the surface to the bottom (30 m). On December 1, two more cod were released with transmitters off Harcourt (Table 1).

On January 9, five cod were caught on longline in Northwest Arm off Weybridge (Fig. 2), sonically tagged, and released. Water temperature was 0.4°C at the surface and 1°C at the bottom (55 m). The final cod was caught, tagged, and released in Random Sound off Southport on January 10.

The cod were fitted with VEMCO Ltd. V3-6HI sonic transmitters (9 cm long × 1.6 cm in diameter, weighing 34 g in air) surgically implanted into the body cavity following the procedures described by Templeman and Fleming (1962) and Lear (1986, 1988). The first cod was anesthetized with ethyl *m*-aminobenzoate or MS-222 (Jolly et al. 1972). Thereafter, no anesthetics were used because the fish caught in 1–2°C waters were lethargic and showed no sign of stress during surgery.

Acoustic Tracking

The V3-6HI transmitter is powered by a lithium battery designed to emit signals for 165 d. Individual fish were identified by frequency (either 65 or 69 kHz) and pulse period (between 965 and 1250 ms) of the transmitter signal. Of the 12 transmitters deployed (Table 1), six had a

TABLE 1. Information on the 12 sonically tagged cod. Fish 1–6 were tagged in Smith Sound, fish 7–11 were tagged in Northwest Arm, fish 12 was tagged in Random Sound, and fish 1, 2, 3, 5, 7, 10, and 11 were still at large as of this writing. The serial number of each transmitter is provided for identification of future recaptures.

Fish No.	Transmitter No.	Length (cm)	Weight (kg)	Date of release	Date recaptured	Place of recapture
1	7692	58	1.3	Nov. 28, 1990	—	—
2	7693	80	5.7	Nov. 28, 1990	—	—
3	7694	64	2.3	Nov. 28, 1990	—	—
4	7695	65	2.3	Nov. 28, 1990	May 3, 1991	Mosquito Cove, Trinity Bay
5	7696	54	1.8	Dec. 1, 1990	—	—
6	7697	64	2.3	Dec. 1, 1990	Nov. 27, 1991	Pass Island, Fortune Bay
7	7715	58	2.0	Jan. 9, 1991	—	—
8	7716	58	2.0	Jan. 9, 1991	Nov. 16, 1991	Northwest Arm, Trinity Bay
9	7717	58	2.0	Jan. 9, 1991	May 27, 1991	Random Sound, Trinity Bay
10	7718	53	1.8	Jan. 9, 1991	—	—
11	7719	47	1.4	Jan. 9, 1991	—	—
12	7720	55	1.8	Jan. 10, 1991	Aug. 10, 1991	Green Island, Bonavista Bay

frequency of 65 kHz and six had 69 kHz. It is possible that two fish with transmitters on the same frequency located together could have confounded their pulse period identifications. However, during the field experiment, fish were usually separated sufficiently such that a directional hydrophone could distinguish individual signals.

Fish were tracked with a VEMCO Ltd. V-10 directional hydrophone attached to the end of a 6-m aluminum pole that was held over the side of the tracking boat and rotated by hand. The maximum range of reception using a V-10 directional hydrophone and a VR-60 receiver was operationally less than 1 nautical mile. The boat was maneuvered to the site of strongest signal reception, and the position of the boat on a navigational chart was determined by using Loran-C, depth soundings, and landmarks.

Attempts were made to relocate the experimental fish as often as costs permitted. The 55-ft. longliner *Northern Quest* was chartered for a total of 33 d between December 5, 1990, and April 11, 1991 (Table 2). No expeditions to the study area were mounted in February.

Measurement of Seawater Temperature

A VEMCO Ltd. Sealog-TD temperature/depth logger with fast response option was used to record the water temperature profile to within 1 m of the sea bottom at each site where a sonically tagged fish was located. The instrument recorded temperature with 0.1°C resolution and an accuracy of ±0.1°C.

Temperature profiles were also measured at stations located along the centre axis of the sounds (Fig. 2). Northwest Arm and Random Sound were surveyed on March 7 (Fig. 3) and April 5. Smith Sound was surveyed on March 8. A temperature survey of Southwest Arm was conducted on April 8 (Wroblewski et al. 1993).

Experimental Fishing

Experimental fishing was conducted (Table 2) to obtain information on the stage of maturity of cod in the study region. Five gill nets each 91.5 m (50 fathoms) in length with 15.25 cm (6 in.) mesh, or a longline consisting of approximately 250 hooks baited with herring, were set out overnight and retrieved the next morning. Cod were weighed, measured for length, sexed, and their reproductive state determined according to the descriptive criteria of Morrison (1990).

TABLE 2. Dates of cruises during the winter 1990–91 study.

Date	Area and operation
Nov. 28	Tagged and released fish 1–4 in Smith Sound
Dec. 1	Tagged and released fish 5 and 6 in Smith Sound; release area in Smith Sound searched for fish 1–4
Dec. 5–6	Smith Sound searched
Dec. 11–12	Smith Sound searched
Jan. 7–13	Northwest Arm, Random Sound, and Southwest Arm searched
Jan. 9	Tagged and released fish 7–11 in Northwest Arm
Jan. 10	Tagged and released fish 12 in Random Sound
Jan. 18–19	Northwest Arm and Random Sound to Smith Sound searched
Jan. 28–31	Northwest Arm, Random Sound, and Southwest Arm searched; experimental fishing near Hatchet Cove, Southwest Arm
Mar. 7–9	Smith Sound, Northwest Arm, Random Sound, and Southwest Arm searched
Mar. 12–15	Northwest Arm, Random Sound, and Southwest Arm searched; experimental fishing near Hickman's Harbour, Hatchet Cove, and in Random Sound
Apr. 5–6	Northwest Arm searched; experimental fishing in Random Sound
Apr. 6	Deep waters of Trinity Bay off Hant's Harbour searched
Apr. 6–11	Experimental fishing near Hatchet Cove
Apr. 8	Southwest Arm searched

Results

Movements of Cod in Winter as Determined by Sonic Tracking

The main purpose of this study was to monitor the movements of cod in response to winter cooling of ocean temperature. Several experimental fish remained inshore throughout the winter (Fig. 4), despite temperatures as low as −1.5°C (Fig. 3).

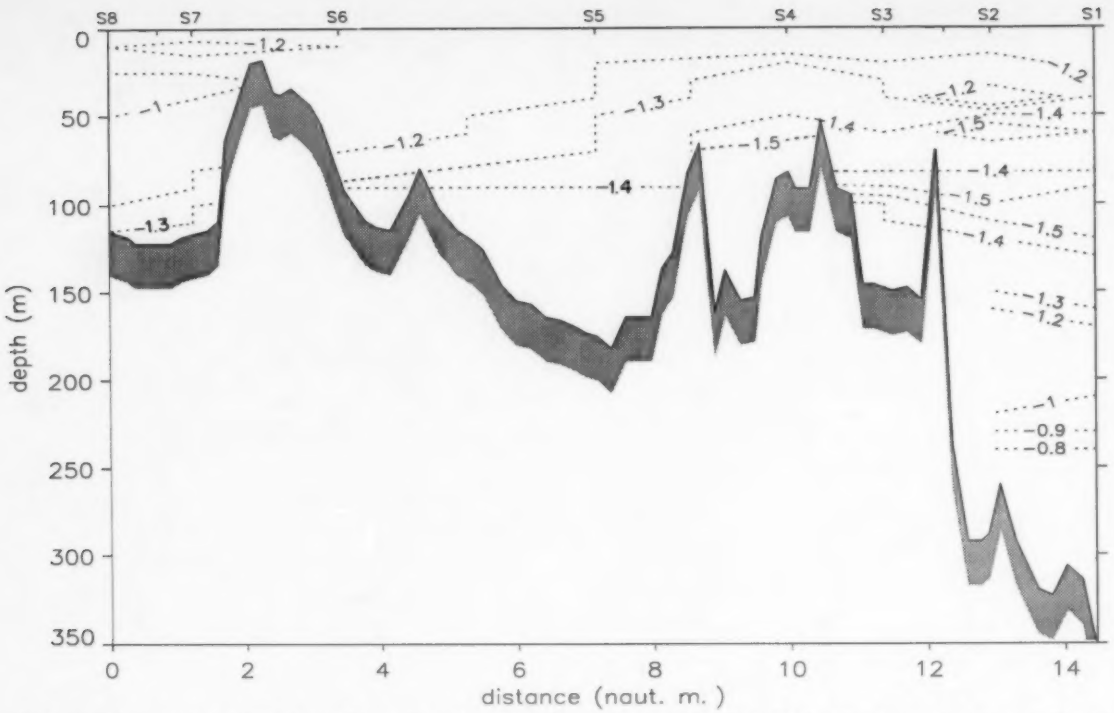

FIG. 3. Temperature section taken along the centre axis of Northwest Arm on March 7, 1991. The deepwater stations S1 and S2 on the right-hand side are in Random Sound. Temperatures were <0°C throughout the sound.

There are grounds in Random Sound and in Northwest Arm that were occupied repeatedly by several fish. A shallow (40 m) knoll in Random Sound off Middle Cliff was frequented by fish 2, 5, and 7. An area outside of Hickman's Harbour was occupied by fish 2, 7, 8, and 9 (Fig. 4). Fish 2 and 5 were relocated together off Middle Cliff on January 19. Fish 2 was detected again off Middle Cliff on January 30 and then relocated on March 15 together with fish 9 on the grounds off Hickman's Harbour (Fig. 4a).

On March 7, fish 8 and 9 were found just outside of Hickman's Harbour (Fig. 4e and 4f). The fish were separated by approximately 100 m. These fish were stationary between March 7 and 13. A temperature profile taken over their position on March 7 (near S4 in Fig. 3) showed −1.1°C at the surface and −1.5°C at the bottom (70 m). On March 13, a longline was laid over the position of fish 8 and 9 in an attempt to catch the cod. No fish were caught (Table 3).

During the winter, no experimental cod were found in the warmest water in the Random Island region which occurred at the bottom of Random Sound (Fig. 3). To pursue Thompson's (1943) suggestion that cod might spend the winter in the deepest part of Trinity Bay, an exploratory survey was made on April 6 across Trinity Bay to the eastern side near Hant's Harbour where water >550 m is located near 48°03′N, 53°21′W. Signals from sonically tagged cod were not detected.

Evidence of Sexually Mature Cod Overwintering Nearshore

Four adult size cod (fish 2, 7, 8, and 9) were tracked from the time of release throughout the winter (Fig. 4). Evidence that other adult cod overwintered in Northwest Arm and Southwest Arm during the winter of 1990–91 was from experimental fishing (Table 3; Fig 5).

The average length of 78 cod caught in January was 55 ± 6 cm. Of 116 cod caught in April, the average length was 60 ± 10 cm. Note (Table 3) that in January, all fish were caught on longline and in April, most fish were caught in gill nets that select for larger fish. No cod were caught during March.

Along the northeast coast of Newfoundland, some cod are sexually mature at <40 cm, 50% are mature at 54 cm, and practically all cod are mature at 65 cm (Fleming 1960). In January, four cod over 65 cm were caught. In April, 35 cod over 65 cm in length were caught.

Table 4 presents the stage of sexual maturity of 153 fish whose gonads were examined between January 29 and April 11. In late January, 39 sexually mature cod were found, including two females with ripe ovaries. In early April, 73 fish were ripening, with four females and two males near spawning. It is clear that both adult and juvenile cod (Fig. 5) were present in the study region during the winter and early spring.

Long-term Survival of Sonically Tagged Cod

Of 12 cod tagged with transmitters, five were caught by fishermen within a year of release (Table 1). Fish 4 released on November 28, 1990, in Smith Sound was caught on May 3, 1991, in a gill net set in 126 m of water at the mouth of Mosquito Cove, Bull Arm, Trinity Bay, approximately 50 nautical miles to the south of our study area (Fig. 1b).

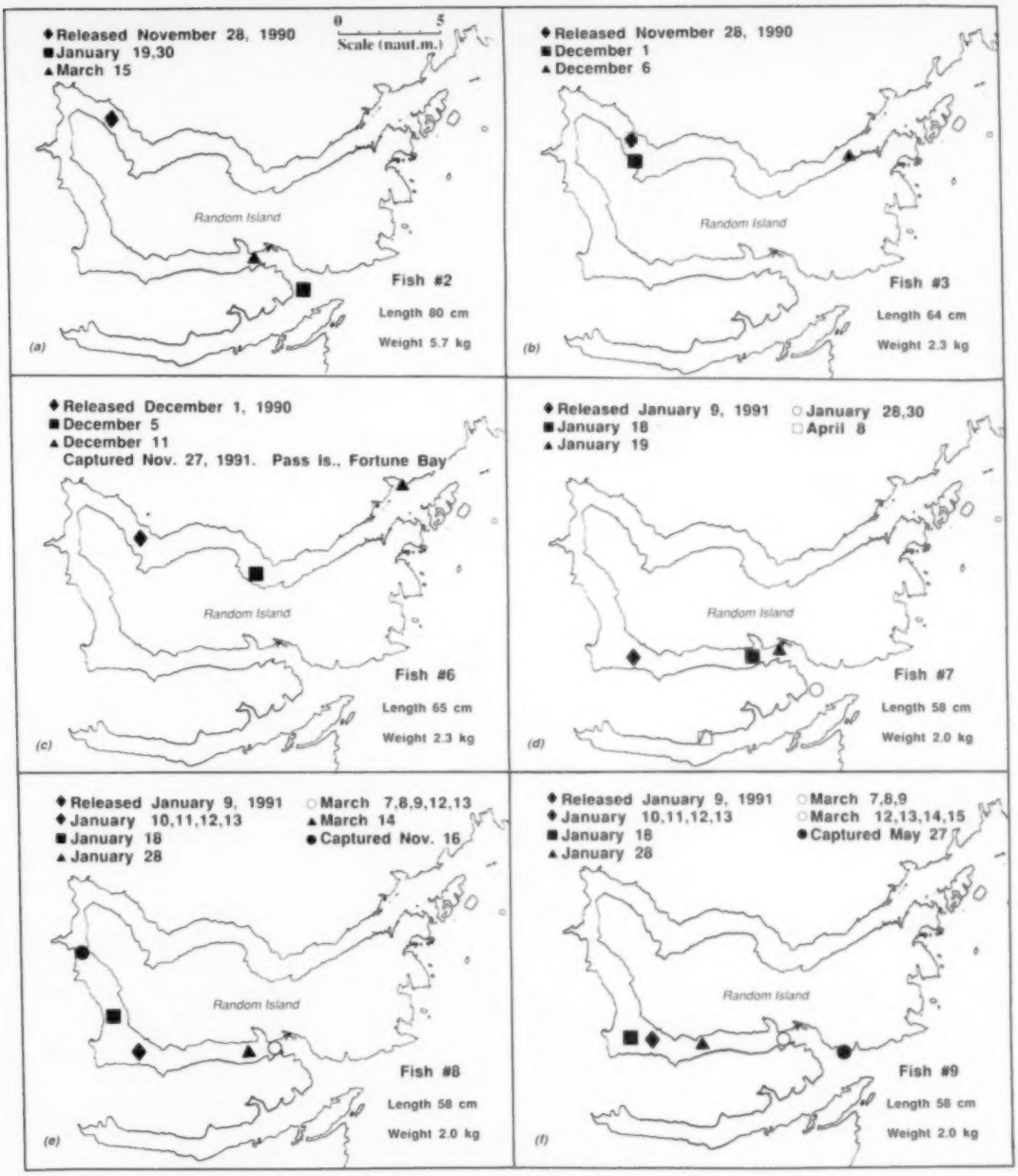

FIG. 4. Sites where sonically tagged cod were relocated within the Random Island region. Fish release points in Smith Sound and Northwest Arm are marked by solid diamonds. (a) Fish 2; (b) fish 3; (c) fish 6; (d) fish 7; (e) fish 8; (f) fish 9. Not shown are fish 5 which was relocated off Middle Cliff in Random Sound on January 19 and fish 10 which remained near the release point in Northwest Arm from January 9 to 28, 1991.

Fish 9, released on January 9, 1991, in Northwest Arm, was caught in a cod trap in Random Sound on May 27 (Fig. 1b and 4f). As fish 9 was captured in the cod trap along with several thousand other cod, this adds to evidence that cod with surgically implanted transmitters can remain healthy. The trap crew returned the gutted fish and transmitter. The fish had a well-healed incision on its side where the transmitter had been implanted in the body cavity. The transmitter taken from fish 9 was still pinging when tested on May 29, 141 d since its battery was activated.

Fish 12, released on January 10, 1991, in Random Sound off Southport, was caught on August 10 off Green Island in Bonavista Bay in a cod trap set in 22 m of water. The fish had traveled approximately 50 nautical miles north-

TABLE 3. Gear type, catch, and bottom temperature during experimental fishing carried out in the Random Island region during winter 1990–91.

Date set–hauled	Depth (m)	Gear	Fishing time (h)	No. of fish	Bottom temperature (°C)
Jan. 28–29	110–165	Longline	18	28	0.4 to 0.7
Jan. 29–30	110–165	Longline	12	27	0.4 to 0.7
Jan. 30–31	110–165	Longline	12	23	0.4 to 0.7
Mar. 13–13	110–165	Longline	8.5	0	−1.3 to −1.4
Mar. 13–14	37–174	Gill nets	15	0	−0.8 to −1.0
Mar. 13–14	18–95	Gill nets	15	0	−0.8 to −1.0
Mar. 14–15	64–128	Gill nets	20	0	−1.1 to −1.4
Mar. 14–15	183–324	Longline	20	0	N/A
Mar. 15–15	128–155	Longline	5	0	−1.4
Apr. 5–6	166	Longline	14	0	−1.3
Apr. 5–6	298	Gill nets	14	0	−0.8
Apr. 6–7	42–166	Longline	17	4	−0.9
Apr. 7–8	180	Gill nets	N/A	10	N/A
Apr. 7–8	238	Longline	12	3	−0.6
Apr. 7–8	152–238	Gill nets	12	44	−0.7
Apr. 8–9	181–219	Gill nets	17	36	−0.7
Apr. 9–10	219	Gill nets	12	11	−0.7
Apr. 10–11	238	Gill nets	12	8	−0.7

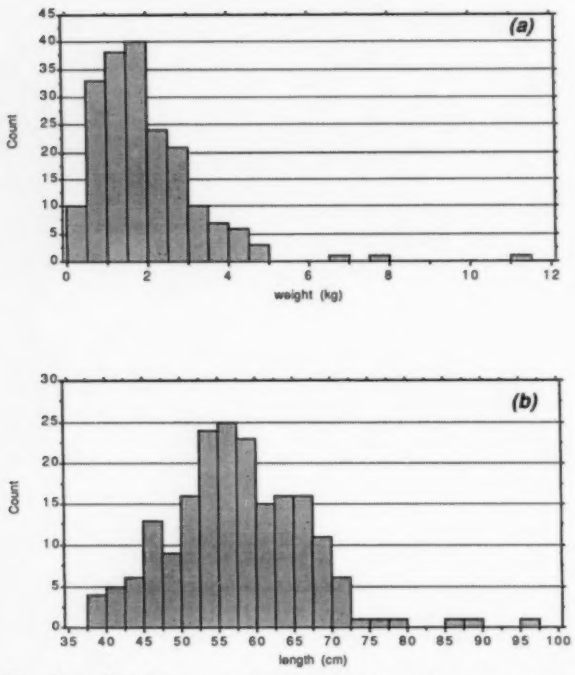

FIG. 5. (a) Weights and (b) lengths of 194 cod that were caught in the study area between January 28 and April 11, 1991 (see Table 3). The mean weight of all fish is 1.88 ± 1.34 kg; the mean length is 57.63 ± 9.20 cm.

ward along the east coast of Newfoundland (Fig. 1b) during the intervening 7 mo.

Experimental fish 8, released on January 9, 1991, in Northwest Arm off Weybridge, was caught on a handline by a fisherman near Clarenville on November 16. This fish was repeatedly located in Northwest Arm during the winter (Fig. 4e).

The fifth fish recaptured was fish 6. This cod was released on December 1, 1990, in Smith Sound and caught by a fisherman almost a year later on November 27, 1991, off Pass Island in Fortune Bay, 305 nautical miles from the point of release (Fig. 1a).

Movements of cod from the east coast to the south coast and vice versa are rare, but do occur (see fig. 5G, 5H, 5I, 6A, 6D, 6G, 11A, 11D, and 11G in Templeman 1979). The surgical incision on this fish was healed with no scar visible to the fisherman who caught the cod. Because the fish was caught on a baited longline, it was likely feeding at the time of recapture.

Discussion

A number of adult northern cod remained inshore during the winter of 1990–91 in the Random Island region of Trinity Bay. Of the 12 cod released with sonic transmitters in the Random Island region during the late fall and early winter, four (fish 2, 7, 8, and 9) appeared to remain inshore throughout the winter (January–March), although there were no observations made in February. Fish that were not relocated in the study region and have not been recaptured since by fishermen (i.e., fish 3, 5, 10, and 11) may have simply been missed during search operations, may have moved to other regions along the coast, or may have moved offshore, as Templeman (1979) suggested.

Why some fish remained inshore is unknown. They may have been part of an inshore–offshore migration where some individuals remained behind at the coast. Alternatively, they may be members of a subpopulation of northern cod that spawns inshore. Templeman's (1979) migration model presumes that the winter–spring location of mature cod is the spawning area.

Instances of fishermen catching cod extruding eggs or milt have been regarded as evidence of spawning in Trinity Bay (Graham 1922). Thompson (1943) stated that any spawning that occurs in Trinity Bay takes place in May and June, occasionally as late as August and September. Results of

egg and larvae surveys in Trinity Bay suggest that spawning occurs in the Random Island region during the summer (E. Dalley, DFO, Box 5667, St. John's, Nfld., unpublished data), but at present there is no evidence of a distinct inshore spawning stock.

Inshore Cod and Winter Ocean Temperatures

Thompson (1943) commented that there may be no necessity for cod to leave Trinity Bay because the local cod can overwinter in the warm slope water in its deepest parts. This study shows adult cod are not excluded by cold temperatures from remaining in the sounds.

In 1965, Templeman and Fleming reported catching a few adult cod in St. Mary's Bay in waters with bottom temperatures of −1.3°C on April 9, 1957. Many juvenile cod but no adult fish were caught during the previous month of February in waters of −1.4°C. This led Templeman and Fleming (1965) to believe that the few adult cod present in April had "returned" to the area and that larger cod evade low temperatures by moving deeper.

These adult cod found in St. Mary's Bay in April may not have returned from deeper water, but indeed may have overwintered there. Moreover, our results are not consistent with Templeman and Fleming's (1965) conclusion that cod are trapped in deep holes that have no passage seaward through which the cod can escape. Ridges in bottom topography did not prevent experimental fish from moving between Smith Sound, Northwest Arm, Random Sound, and Southwest Arm (Fig. 4a, 4d, and 4f).

Early Spring Inshore Fishery

The recapture of two sonically tagged fish by local fishermen contributes to evidence that adult cod remain nearshore through the winter and become available to the inshore fishery in the early spring before the main body of offshore cod arrives at the coast. Fish 4 was caught in a gill net near Mosquito Cove on May 3. Fish 9 was caught in a cod trap in Random Sound on May 27 along with 5000 kg of other cod caught by the crew on that day. When this study began, many local fishermen believed that cod move out of the area in the winter and return in the spring. Sonic tracking has demonstrated that some cod remained through the winter of 1990–91.

Tagging work concurrent with our study found that cod present in Southwest Arm in January 1991 were caught by local fishermen that spring (C. Taggart, DFO, Box 5667, St. John's, Nfld., unpublished data). Tagged with Peterson discs and spaghetti T-bar labels, 2690 cod ranging from 35 to 80 cm in length were released in Southwest Arm. By the end of May, fishermen in the Random Island area caught 319 of these cod. Most were caught in cod traps set at depths <50 m or in gill nets set at depths <250 m. The average size of these fish was 48.4 cm. Twenty-six of the 116 cod caught by our experimental fishing in April (Table 3) had these tags.

From tagging studies, Templeman (1979) found that many of the adult cod released inshore along the east coast of Newfoundland during the fall months (October–December) were caught by fishermen tens to hundreds of miles away but still near the coast during the fall, winter, and spring of subsequent years. Based on our results, we suggest that these tagging data contain earlier (albeit indirect) evidence that adult cod overwinter nearshore and are available to the early spring inshore fishery.

TABLE 4. Sexual maturity stage (descriptive criteria of Morrison 1990) of cod caught during experimental fishing. Stage 0 is immature, 1 is ripening, 2 is ripe and spawning, and 3 is spent.

Date	Sex	No. of fish	Condition			
			0	1	2	3
Jan. 29	Male	9	2	7	0	0
	Female	17	8	8	1	0
Jan. 30	Male	10	2	8	0	0
	Female	16	7	8	1	0
Jan. 31	Male	7	7	0	0	0
	Female	8	2	6	0	0
Apr. 7	Male	1	1	0	0	0
	Female	1	0	1	0	0
Apr. 8	Male	11	1	8	2	0
	Female	21	1	18	2	0
Apr. 9	Male	17	1	16	0	0
	Female	19	2	15	2	0
Apr. 10	Male	3	0	3	0	0
	Female	8	2	6	0	0
Apr. 11	Male	1	0	1	0	0
	Female	6	1	5	0	0

Acknowledgments

We wish to thank the crew of the *Northern Quest* and the community of Hickman's Harbour for assisting us in our field research. Drs. Henry Lear, John Green and Geoff Arnold provided advice on sonically tagging and tracking of cod. Mr. Allan Collier analyzed the temperature data. We dedicate this paper to the memory of Mr. Alfred Andrews, who encouraged us to begin a study of Random Island cod. Funding for this research has been provided by the Natural Sciences and Engineering Research Council of Canada (NSERC), National Sea Products Ltd., and Fishery Products International Ltd. under NSERC's Research Partnerships Program.

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Zooplankton Communities and Water Chemistry of Sudbury Area Lakes: Changes Related to pH Recovery

Andrea Locke[1] and W. Gary Sprules

Department of Zoology, Erindale Campus, University of Toronto, Mississauga, ON L5L 1C6, Canada

W. Keller

Ontario Ministry of Environment and Energy, 199 Larch St., Sudbury, ON P3E 5P9, Canada

and J. Roger Pitblado

Geography Department, Laurentian University, Sudbury, ON P3E 2C6, Canada

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Temporal trends in pH, alkalinity, and crustacean zooplankton species richness and community composition were studied in 80 Sudbury area lakes sampled in 1971–76, 1981, and 1988–90. Alkalinity and pH have increased in recent years, but many of the study lakes remain quite acidic (modal pH 4.5–4.9). Species richness has also increased, on average, by 1.9 species/lake but is still low in many acid lakes relative to that in circumneutral lakes. Community composition differed among lakes of pH <5.0, 5.0–5.9, and ≥6.0, with some overlap between these groups because zooplankton recovery has lagged behind chemical recovery. Trajectories of community change in recovering acid lakes varied substantially in the early stages of recovery from highly acidic (pH <5.0) to moderately acidic pH (5.0–5.9). In contrast, trajectories in lakes recovered to pH ≥6.0 converged toward the community structure more typical of circumneutral lakes in the 1970's. This suggests that given sufficient time, zooplankton community structure of recovering lakes may approach that of circumneutral lakes.

Nous avons étudié les tendances temporelles du pH, de l'alcalinité, de la richesse spécifique des crustacés zooplanctoniques et de la composition des communautés dans 80 lacs de la région de Sudbury échantillonnés en 1971–1976, 1981 et 1988–1990. L'alcalinité et le pH ont augmenté ces dernières années, mais bon nombre des lacs étudiés restent plutôt acides (pH moyen 4,5–4,9). La richesse spécifique a aussi augmenté, en moyenne de 1,9 espèce/lac, mais est faible dans de nombreux lacs acides par rapport à celle des lacs pratiquement neutres. La composition des communautés différait entre les lacs selon qu'ils avaient un pH < 0,5, entre 5,0 et 5,9 et ≥ 6,0, avec un certain chevauchement entre ces catégories du fait que le rétablissement du zooplancton est en retard par rapport au rétablissement sur le plan chimique. La courbe du changement des communautés dans les lacs acides en voie de rétablissement variait fortement dans les premières étapes du rétablissement selon que les eaux étaient fortement acides (pH < 5,0) ou modérément acides (pH 5,0–5,9). Par contre, dans les lacs ayant retrouvé un pH ≥ 6,0, les tendances convergeaient vers une structure des communautés plus typique des lacs pratiquement neutres dans les années 1970. Cela semble indiquer que, si le temps est suffisamment long, la structure communautés se zooplancton dans les lacs en voie de rétablissement pourrait se rapprocher de celle des lacs presque neutres.

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Severe acidification of lakes, resulting from smelter emissions, was initially recognized in the vicinity of Sudbury, Ontario, three decades ago (Gorham and Gordon 1960). However, acidic atmospheric emissions in the Sudbury area have declined in recent years (from 2.2×10^6 tonnes (t)/yr in 1950–1972 to 0.68×10^6 t/yr in 1979–85; Dillon et al. 1986) and substantial reductions in lake acidity have been documented (Keller et al. 1986, 1992b). These improvements in water quality have been accompanied by recoveries of phytoplankton (Dixit et al. 1989, 1992; Nicholls et al. 1992), zooplankton (MacIsaac et al. 1986; Gunn and Keller 1990; Keller and Yan 1991), zoobenthos (Gunn and Keller 1990; Griffiths and Keller 1992), and lake trout, *Salvelinus namaycush* (Gunn and Keller 1990). However, documentation and understanding of biological recovery from acid stress are still limited. For zooplankton, the patterns of recovery were examined in only eight Sudbury area lakes. In this paper, we extend the assessment of zooplankton recovery to 80 lakes in the Sudbury area. Such documentation is essential for assessing the effects and adequacy of emission control programs in the Sudbury area and elsewhere.

The lakes included in our study were initially surveyed in 1971–73 (Sprules 1975) or 1974–76 (Keller 1981). In this paper, we evaluate recent changes in water chemistry (pH and alkalinity) and crustacean zooplankton communities (species richness and taxonomic composition) of these lakes.

[1]Present address: Department of Fisheries and Oceans, Marine and Anadromous Fish Division, Gulf Fisheries Centre, P.O. Box 5030, Moncton, NB E1C 9B6, Canada.

TABLE 1. Selected characteristics of the study lakes. Total inflection point alkalinity is shown for 1988 or 1990, as available. Where Z_{max} is unknown, maximum depth of sampling is presented.

Lake	Latitude (N)	Longitude (W)	Area (ha)	Z_{max} (m)	pH					Alkalinity, 1988–90 (μeq/L)
					1971–73	1974–76	1981	1988	1990	
Acid	46° 2′	81°26′	17.7	30.0	4.8				5.2	5.96
Annie	46°11′	81° 8′	202.8	≥17.7		5.2	5.3	5.7		0.66
Aurora Whitepine	47°23′	80°38′	77.8	21.3			5.8	4.9		−0.62
A.Y. Jackson	46° 2′	81°24′	6.1	9.8	5.0				6.2	31.81
Bell	46° 8′	81°12′	281.3	26.8	5.2	5.4	5.4	5.6	6.1	32.82
Bluesucker	47°10′	80°37′	144.6	21.3			5.1	5.4		0.14
Bob	47°10′	80°16′	161.1	25.0		4.6	4.8	5.1		−0.10
Bodina	46° 6′	81°30′	30.3	6.7	6.3				7.0	127.75
Boundary	46° 8′	81°19′	74.1	9.8	4.2				5.2	12.12
Carlyle	46° 4′	81°13′	166.9	14.6	5.0				6.6	20.99
Charlton	46° 9′	81°42′	218.9	18.0	6.2				6.6	120.97
Chiniguchi	46°56′	80°42′	1511.0	45.0		4.4	4.6	4.9		−0.60
Clearsilver	46° 7′	81°15′	23.9	13.7	4.3				4.8	7.66
Clearwater	46°22′	81° 3′	76.9	21.5		4.4	4.5	4.7		−1.10
David	46° 8′	81°18′	325.8	24.4	4.6	4.6	4.7	4.8	4.9	4.69
deLamorandiere	46° 2′	81°27′	5.3	7.6	5.0				5.1	4.43
Donald	46°48′	80°31′	459.9	60.0		4.6	4.7	4.8		−0.73
Dougherty	47° 1′	80°40′	317.5	53.8			4.5	4.7		−1.10
Evangeline	48° 8′	81°52′	384.9	19.2	5.9	6.3	6.6		6.3	104.18
Fish	46°10′	81°24′	90.7	8.5	5.7				6.2	38.18
Florence	47°15′	80°33′	1006.9	22.0		4.5	4.8	5.0		−0.40
Fraleck	46°55′	80°55′	173.9	23.4		5.3	5.8	5.7		0.99
Frederick	47° 2′	80°44′	174.1	21.0		4.5	4.6	4.8		−0.74
Freeland	46° 2′	81°22′	32.2	1.8	4.2				6.0	33.96
Frood	46° 8′	81°42′	191.8	18.0	5.9				7.0	170.35
Gail	46° 9′	81°22′	16.6	16.8	3.8				4.6	−8.32
Gem	46° 9′	81°26′	14.2	19.2	6.1				6.6	63.27
George	46° 2′	81°24′	147.9	30.5	4.9	5.2	5.4	5.7	6.4	11.06
Great Mountain	46° 7′	81°21′	191.6	37.5	4.4				5.2	13.39
Gullrock	47°19′	79°56′	217.9	12.8		4.6	5.2	5.8		0.64
Helen	46° 7′	81°34′	68.2	41.2	7.0	5.4	6.6		7.0	96.91
Howry	46° 9′	81°28′	101.9	27.4	6.0				6.8	72.18
Ishmael	46° 7′	81°36′	65.4	19.8	6.4				7.0	142.75
Jim Edwards	47°16′	80°26′	82.6	≥19.1		4.6	4.9	5.1		−0.18
Johnnie	46° 6′	81°18′	395.5	33.5	5.1		4.5	4.7	5.3	4.52
Kakakise	46° 4′	81°20′	118.9	30.5	5.6				6.5	27.57
Killarney	46° 4′	81°21′	357.2	61.0	4.7		4.9	5.0	5.6	7.16
Klock	47°28′	80° 8′	145.7	14.0		4.7	4.9	5.3		−0.10
La Cloche	46° 8′	82° 4′	1088.3	30.5	6.0				7.0	73.79
Landers	47°16′	80°29′	108.3	≥12.7		4.6	4.8	4.8		−0.42
Laundrie	47° 7′	80°52′	364.4	20.4		4.7	5.2	5.5		0.39
Little Mountain	46° 9′	81°22′	20.0	25.0	4.4				4.8	3.31
Little Sheguindah	46° 2′	81°23′	5.0	2.7	5.0				6.1	39.68
Little Superior	46° 5′	81°20′	12.1	33.5	4.5				4.4	422.63
Logboom	46° 7′	81°14′	6.0	6.0	5.3				5.3	28.44
Low	46° 6′	81°34′	28.6	28.4	7.0				7.2	305.00
Lumsden	46° 1′	81°26′	21.5	22.9	4.4				5.2	3.24
Mahzenazing	46° 3′	81°11′	95.4	≥16.3			5.5	5.6		0.73
Marjorie	46°55′	80°37′	77.4	35.0			4.3	4.5		−2.10
Matagamasi	46°47′	80°36′	1392.7	61.5		4.6	4.9	5.2		−0.08
Muriel	45° 6′	81°26′	22.6	12.2	4.8				6.0	13.06
Nellie	46° 8′	81°32′	238.3	54.9	4.1	4.4	4.5	4.6	4.6	−4.98
Norway	46° 5′	81°19′	59.6	33.6	4.7				5.1	8.17
O.S.A.	46° 4′	81°24′	291.4	39.7	4.8	4.5	4.6	4.8	5.2	0.52
Partridge	46° 5′	81°18′	9.2	16.8	5.2				5.1	−1.51
Patten	46° 7′	81°21′	8.7	6.4	6.0				5.2	3.92
Pilgrim	47°11′	80°41′	129.6	25.0			5.2	5.7		0.30
Proulx	46° 5′	81°20′	10.5	28.7	4.6				4.6	−3.45

TABLE 1. (*Concluded*)

Lake	Latitude (N)	Longitude (W)	Area (ha)	Z_{max} (m)	pH					Alkalinity, 1988–90 (μeq/L)
					1971–73	1974–76	1981	1988	1990	
Reef	46°15′	81°12′	227.0	33.8		4.7	5.2	5.7		−0.02
Roque	46° 1′	81°28′	3.4	10.1	4.9				5.1	−5.49
Ruth-Roy	46° 5′	81°15′	46.1	18.0	4.5		4.6	4.7	5.1	6.32
Seagram	47° 6′	80°32′	81.0	20.0			5.1	5.4		0.33
Shingwak	46° 5′	81°19′	4.6	21.6	4.6				4.8	1.23
Silver	46°26′	81° 1′	19.4	10.0			4.1	4.2		−3.20
Silvester	45°51′	80°39′	50.6	≥10.0			4.5	4.7		−1.00
Solomon	46° 2′	81°27′	5.2	4.9	5.0				6.0	15.39
Sunnywater	47°24′	80°37′	141.7	≥51.5		4.4	6.1	4.7		−0.88
Telfer	46°57′	80°47′	305.7	34.1		4.8	4.8	5.0		−0.41
Terry	46° 4′	81°17′	10.1	8.0	4.2				5.9	26.49
Threenarrows	46° 6′	81°26′	947.9	51.9	5.2	5.0	5.7		6.5	37.12
Tillie	47° 3′	81° 0′	65.3	≥9.8			4.9	5.3		0.90
Turbid	46° 7′	81°11′	14.8	9.4	4.6				5.6	13.33
Tyson	46° 7′	81° 7′	1142.7	39.6		5.3	5.3	5.6		0.72
Wabun	47°25′	80°36′	55.0	≥31.5		4.7	4.8	5.0		−0.29
Wavy	46°18′	81° 6′	255.1	34.0		4.5	4.7	4.8		−0.79
Welcome	47°13′	81° 2′	669.2	27.7		6.6	6.7	6.8		5.81
Whiskeyjack	46° 5′	81°18′	13.8	42.7	4.2				4.8	−2.81
White Oak	46°18′	81° 0′	305.0	43.0		4.8	5.0	5.2		−0.06
Whitson	46°35′	80°58′	437.7	16.2		4.8	5.2	5.9		2.07
Wolf	46°52′	80°38′	79.8	≥51.0		4.3	4.5	4.8		−0.93

Data collected in the original surveys were compared with data collected in 1981 (Keller and Pitblado 1984) and 1988 for lakes in the original Keller survey and in 1990 for lakes in Sprules' original dataset.

Methods

Data Collection

The 80 lakes included in the study (Table 1) are located on the Precambrian Shield in northeastern Ontario, within 165 km of Sudbury. Physicochemical data will be presented in W.G. Sprules et al. (in preparation).

None of the study lakes has been directly subjected to experimental manipulations of water chemistry, although Laundrie Lake is located downstream of Bowland Lake, which was experimentally neutralized in 1983 (Molot et al. 1990). A substantial reduction in acidity had already occurred in Laundrie Lake (from pH 4.7 in 1974–76 to pH 5.2 in 1981), but pH subsequent to 1983 probably reflects the effect of upstream neutralization.

Data were assembled from several sources (Sprules 1975; Keller 1981; Keller and Pitblado 1984; and surveys by W. Keller in 1988 and by A. Locke and W.G. Sprules in 1990). In total, the lakes were sampled in at least two of three periods: 1971–76, 1981, and 1988–90 (35 lakes were sampled throughout, 35 in 1971–76 and 1988–90 only, and 10 in 1981 and 1988–90 only; Table 1).

Sprules (1975) sampled zooplankton and water chemistry once in each lake from July to early September 1971–73. Zooplankton were collected with nets of 25- to 30-cm mouth diameter and 75- to 110-μm mesh size. Samples were collected during daylight hours using a single vertical haul from near-bottom to surface in each major basin at the point of maximum depth. A horizontal haul was substituted in shallow lakes. In multibasin lakes, zooplankton abundances and chemistry were averaged.

Keller (1981) sampled lakes in daylight hours between May and October 1974–76. One basin of each lake was visited one to seven times, and samples from all dates were pooled for analysis. Vertical net hauls from 1 m above the sediments to the water surface (or from 2× Secchi depth to surface, in 13 lakes) were used to collect zooplankton. Nets used were 11–20 cm in diameter with 76- to 80-μm mesh.

Each lake in the study of Keller and Pitblado (1984) was sampled once at a central location in June–August 1981, using a single vertical haul (from 1 m above the sediments to the water surface) of a 12.5-cm-diameter net with 76-μm mesh. The same methods were used when these lakes were resampled in June–August 1988.

In 1990, the lakes initially sampled by Sprules (1975) were sampled once during daylight hours in August. Three net hauls from near-bottom to surface were collected at the deep point of each lake and pooled for further analysis; each basin of multibasin lakes was sampled and data were averaged. In shallow lakes, a horizontal tow was substituted. The net used was 25 cm in diameter with mesh size of 76 μm.

Crustacean zooplankton abundance and water chemistry data from the five surveys were combined into a dataset encompassing three periods, 1971–76, 1981, and 1988–90. Abundance and water chemistry data were averaged if a lake was sampled more than once during a time period. Taxonomic discrepancies between the surveys were minimized when possible, for example by reidentifying bosminid species from the 1971–73 survey (when all bosminids were identified as *Bosmina longirostris*). Changes in *Diaphanosoma* taxonomy over time necessitated the pooling of all *Diaphanosoma* spp. Abundances of *Daphnia pulex* and *Daphnia pulicaria* were also pooled. Immature copepodids and nauplii were omitted from the analysis because these taxa were not identified to species.

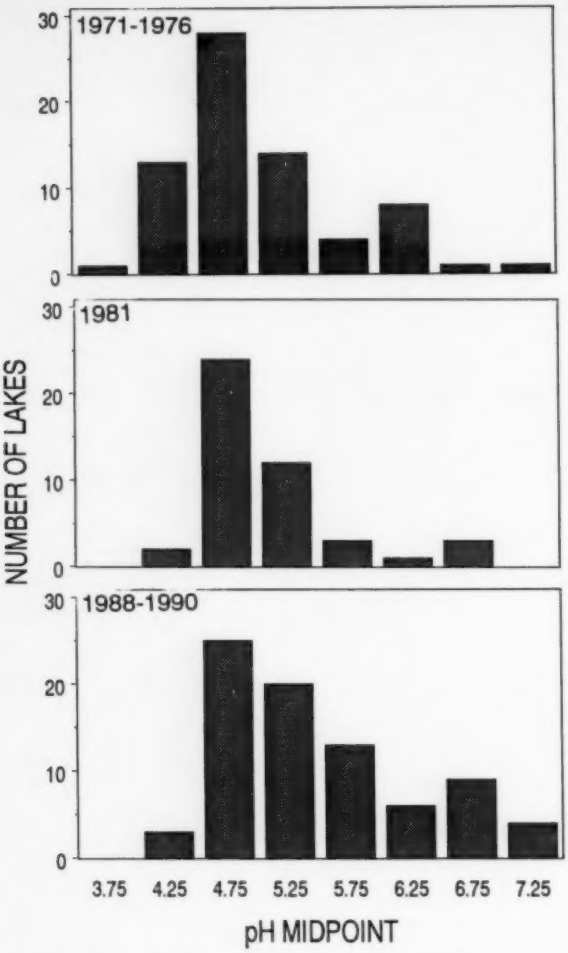

FIG. 1. pH distributions of lakes sampled in 1971–76, 1981 and 1988–90.

Data Analysis

Contingency analysis (following Zar 1984) was used to compare the numbers of lakes with pH in three categories (highly acidic, pH below 5.0; moderately acidic, pH between 5.0 and 5.9; and circumneutral, pH 6.0 and above) in 1971–76, 1981, and 1988–90. These pH categories were chosen, since 5.0 is believed to be a critical pH value for zooplankton composition (e.g., Sprules 1975), yet significant biological damage has been documented for lakes with pH below 6.0 (Schindler 1988; Keller et al. 1990; Matuszek et al. 1990). Because different sets of lakes were sampled in each of the three periods, three separate contingency analyses were performed, comparing 1971–76 with 1988–90, 1971–76 with 1981, and 1981 with 1988–90 data.

Geometric mean regression (Ricker 1984) was used to investigate trends in total inflection point alkalinity of lakes sampled in 1981 and 1988–90 (total inflection point alkalinity was not measured in 1971–76). For this analysis, we utilized a BASIC program written by K. Somers (Ontario Ministry of Environment and Energy, P.O. Box 39, Dorset, ON, P0A 1E0). We used *t*-tests to test the significance of the intercepts and slopes of the regressions.

Crustacean species richness (number of taxa per lake) was also analysed by geometric mean regression, comparing data from 1971–76 and 1988–90. The analysis was conducted in the same way as the alkalinity regression. A bootstrapping procedure was used to produce 5 and 95% quantile values for the intercept and slope of the regression, in order to verify the results of the *t*-tests.

To determine the effects of changes in sampling protocols over time on the observed species richness, we looked at the number of lakes with increased, decreased, or unchanged species richness in each of the two data series used in the study, comparing 1970's data with those of 1988–90. Because Keller (1981) sampled lakes as many as seven times between 1974 and 1976, pooling samples from all dates for analysis, but thereafter sampled on only one date during each sampling period, species richness might have been biased toward higher values in the 1974–76 survey. Lakes from Sprules' (1975) dataset were sampled on only one occasion in 1971–73 and again in 1990, but a larger volume of water was sampled in 1990, which might have biased species richness toward higher values in the later survey (although probably not as much as sampling on several dates would have). Further, a longer time had elapsed between the original and most recent surveys of the Sprules lakes (17–19 yr) than the Keller lakes (12–14 yr), with the potential for more recovery to have taken place in the former lakes. A contingency table analysis was used to compare trends in the two surveys.

Zooplankton community composition was examined using two ordination techniques, principal components and correspondence analyses, as calculated by SAS version 6.06 (SAS Institute, Inc., 1990). Similar patterns were obtained from each ordination technique and we present only the results of the principal components analysis (PCA). All lakes and dates were analysed simultaneously, using the correlation matrix of log-transformed abundances of species found in at least 10% of the samples (the cladocerans *Bosmina longirostris, Chydorus sphaericus, Daphnia ambigua, Daphnia catawba, Daphnia galeata mendotae, Daphnia longiremis, Daphnia pulex, Daphnia retrocurva, Diaphanosoma* spp., *Eubosmina longispina, Eubosmina tubicen, Holopedium gibberum, Leptodora kindti*, and *Polyphemus pediculus*, the calanoid copepods *Diaptomus reighardi, Epischura lacustris, Leptodiaptomus minutus*, and *Skistodiaptomus oregonensis*, and the cyclopoid copepods *Diacyclops thomasi, Mesocyclops edax*, and *Tropocyclops prasinus*). Pearson's product-moment correlations of log-transformed abundances and untransformed physicochemical variables with the first two principal component axes were computed. Trajectories of community change were examined by separately plotting the ordinations of lakes which had recovered from pH < 5.0 to pH 5.0–5.9 and from pH < 6.0 to pH ≥ 6.0.

Results

pH and Alkalinity

Hydrogen ion concentrations in the study lakes have decreased since the 1970's although many lakes remain quite acidic. Modal pH (4.5–4.9) has not changed (Fig. 1),

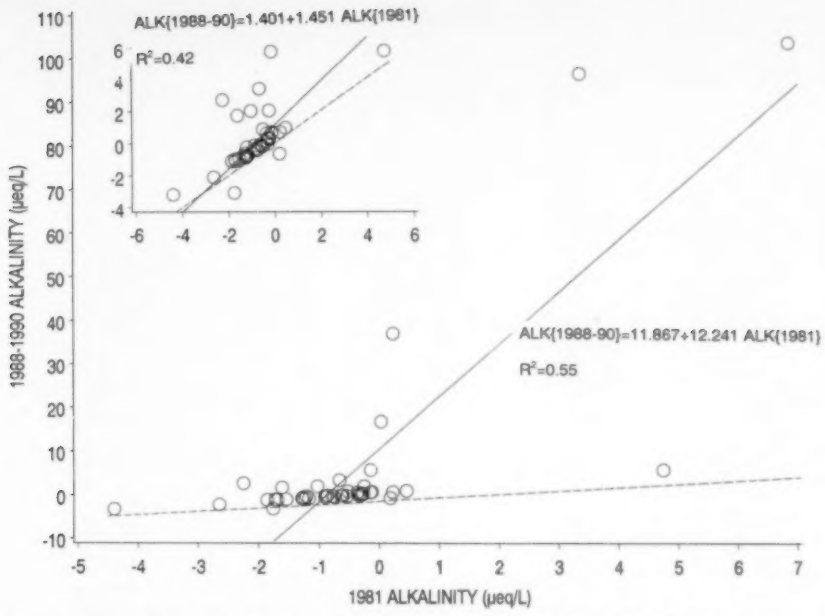

FIG. 2. Change in total inflection point alkalinity from 1981 to 1988–90. The broken line represents a 1:1 relationship. The sold line is a geometric mean regression of 1988–90 on 1981 data. The inset shows the effect of removing four outlying points.

but geometric mean pH has increased from 4.65 (1971–76) to 4.81 (1981) to 5.06 (1988–90). This is reflected in significant recent improvements in pH in lakes sampled in 1971–76 and 1988–90 (Table 2a). No significant change in pH distribution was detected when comparing 1971–76 with 1981 (Table 2b) and 1981 with 1988–90 (Table 2c), but selection of the 42 lakes sampled in 1981 was determined by pH < 5.5 in 1974–76, and thus this subsample is probably not representative of the whole dataset.

Improvements in acid-neutralizing capacity from 1981 to 1988–90 are indicated by the regression of total inflection point alkalinities (Fig. 2) in which the slope (b = 12.24) was greater ($P < 0.05$) than 1 (a slope of 1 and intercept of 0 indicates no change over time). In this dataset, four lakes with 1988–90 alkalinities of 16.8 to 104.2 μeq/L strongly influenced the calculated slope, and the regression analysis was repeated excluding these lakes. The slope (b = 1.45) of this regression was still significantly greater than 1 (Fig. 2).

Species Richness

Zooplankton species richness also increased from 1971–76 to 1988–90 (Fig. 3). The slope of the regression (b = 1.12) was not significantly different from 1, but the intercept (1.86) was greater ($P < 0.05$) than 0; thus, species richness improved overall, and the rate of increase was similar in all lakes. This result was verified by bootstrapping (5 and 95% quantiles of the intercept were 0.83 and 3.27, i.e., the value 0 was not included in this interval, and those of the slop were 0.88 and 1.27, i.e., the value 1 was included in this interval, supporting the results of the t-tests). Therefore the intercept of the regression equation, 1.9 species/lake, represents the average increase in species richness from 1971–76 to 1988–90.

TABLE 2. Distribution of pH values among lakes in 1971–76, 1981, and 1988–90.

(a) Comparison of pH of 70 lakes sampled in 1971–76 and 1988–90 (χ^2 = 7.74, $P < 0.05$)

	Number of lakes	
pH	1971–76	1988–90
<5.0	42	23
5.0–5.9	18	28
≥6.0	10	19

(b) Comparison of pH of 35 lakes sampled in 1971–76 and 1981 (χ^2 = 1.24, $P > 0.05$)

	Number of lakes	
pH	1971–76	1981
<5.0	25	21
5.0–5.9	8	10
≥6.0	2	4

(c) Comparison of pH of 45 lakes sampled in 1981 and 1988–90 (χ^2 = 0.89, $P > 0.05$)

	Number of lakes	
pH	1981	1988–90
<5.0	26	21
5.0–5.9	15	20
≥6.0	4	4

Trends over time in species richness were different ($P < 0.05$) in the two studies (Table 3a). Increased species richness was more common in lakes originally surveyed by

TABLE 3. Comparison of trends in species richness from the 1970's to 1988–90 in lakes originally sampled by Keller in 1974–76 and Sprules in 1971–73 ($\chi^2 = 11.64$, $P < 0.005$) and distribution of lakes between pH categories.

(a) Comparison of trends in species richness

Survey	No. of lakes in which species richness: increased	decreased	did not change
Keller	10	4	6
Sprules	40	3	3

(b) Distribution of lakes between pH categories

Survey	Year	Percentage of lakes with: pH < 5.0	pH of 5.0–5.9	pH ≥ 6.0
Keller	1974–76	80	15	5
Keller	1988	43	57	0
Sprules	1971–73	48	32	20
Locke and Sprules	1990	26	35	39

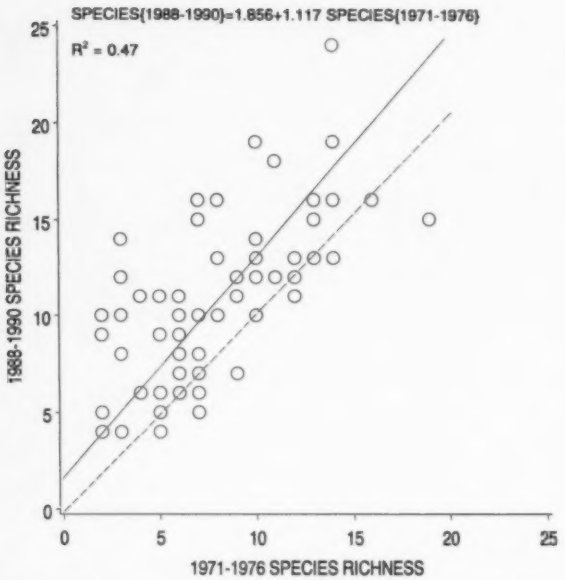

FIG. 3. Change in zooplankton species richness from 1971–76 to 1988–90. The broken line represents a 1:1 relationship. The solid line is a geometric mean regression of 1988–90 on 1971–76 data.

Sprules than in those sampled by Keller. However, the distribution of pH in the two studies also differed (Table 3b), with more lakes in Sprules' dataset having recovered to circumneutral pH in the recent survey.

Community Composition

The first axis (24.4% of variance explained) of the PCA of zooplankton abundances provided good resolution of lakes with pH less than 6.0 from those of pH 6.0 or higher (Fig. 4). Lakes with pH below 5.0 and those with pH of 5.0–5.9 were only partially separated. Highly significant ($P < 0.0001$) positive correlations of pH, alkalinity, and longitude with PCA scores on axis 1 and negative correlations of sulfate concentration and latitude (Table 4) suggest that pH-related phenomena are strongly associated with the position of lakes along that axis. Latitude and longitude are important because they combine the effects of distance from Sudbury (a nonsignificant correlation) and position relative to prevailing winds. Lakes with high scores on axis 1 also had higher nutrient (N, P) levels as well as higher Fe, Si, and K concentrations. Lakes with lower scores were more transparent and of higher elevation (Table 4). High scores on axis 1 were also positively correlated with abundances of nine of the 14 cladoceran species included in the analysis, all four calanoids, and all three cyclopoids (Table 4). Only *Eubosmina longispina* was associated with acidic lakes, i.e., there was only one negative correlation (Table 4). The occurrence of an axis with correlations (eigenvectors) all of the same sign indicates size rather than shape relationships in morphometric analyses (Pimentel 1979); the analogous situation in community analysis is that shifts in abundance rather than taxonomic composition are explained. Thus, the distribution of lakes on axis 1 primarily reflects differences in overall abundance of zooplankton along the pH gradient, with most species being collected both more frequently (Table 5) and in greater abundance (Table 6) in lakes of higher pH. In other words, acidification resulted in attrition of the existing community rather than its replacement by a new set of organisms. An additional PCA utilizing arcsine transformed relative abundance data yielded very similar results to that utilizing absolute abundance, with the only major difference being that the relative abundance of *Leptodiaptomus minutus* was negatively correlated with axis 1, i.e., this species represented a greater proportion of the community in acidic than in circumneutral lakes.

Axis 2 of the PCA was distorted into an arch configuration. This configuration results from a quadratic distortion of the valid first PCA axis, indicating that species abundances do not change linearly along underlying gradients (Gauch 1982; James and McCulloch 1990). Axis 2 thus conveyed little useful information. A correspondence analysis per-

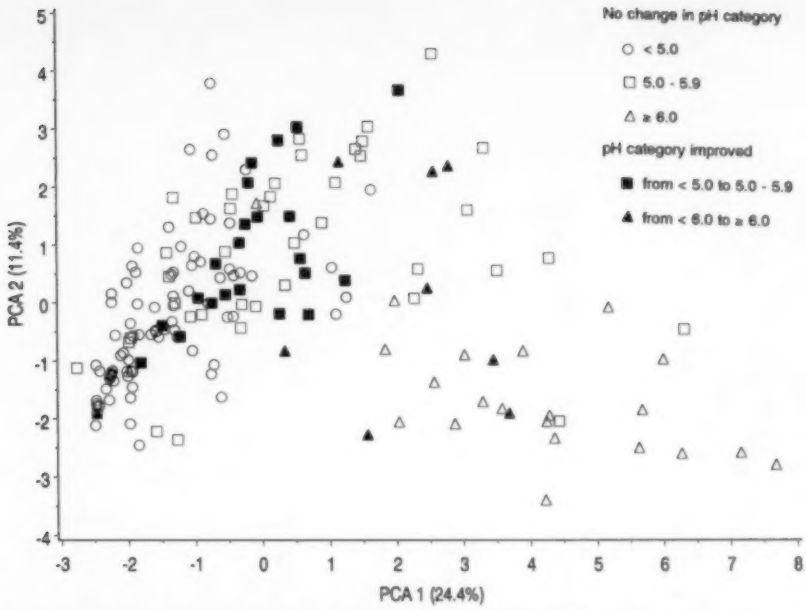

FIG. 4. Ordination of lakes on the first two axes of PCA of logged zooplankton species abundances. Closed symbols represent "recovering" lakes in 1981 and/or 1988–90, i.e., those in which pH has recovered from acidic or highly acidic to circumneutral, or from highly acidic to acidic, since the previous sampling period. Open symbols represent initial lake conditions in 1971–76, or lakes which were not "recovering" in 1981 or 1988–90.

formed on these data (A. Locke, unpublished data) confirmed the trends observed on axis 1 and the limited usefulness of succeeding axes.

Much of the observed overlap between groups on axis 1 was due to "recovering" lakes, i.e., those which had been members of a lower pH category in an earlier time period. For example, four lakes with pH ≥ 6.0 which were ordinated among the pH 5.0–5.9 lakes, based on their zooplankton composition, had had pH in the range of 5.0–5.9 in the previous sampling period.

Trajectories of community change in recovering lakes were very diverse for lakes recovering to pH 5.0–5.9 (Fig. 5a), but less so for lakes recovering to pH ≥ 6.0 (Fig. 5b). PCA scores of lakes in the latter category generally increased on axis 1 and decreased on axis 2, i.e., the recovering lakes became more similar to those having pH ≥ 6.0 in the 1971–76 surveys.

TABLE 4. Significant (P <0.05, *P < 0.0001) correlations of lake physicochemical data and logged species abundances with first PCA axis.

Positive correlations	Negative correlations
pH*	Secchi depth*
Total inflection point alkalinity*	Elevation*
Longitude*	Latitude*
Total Kjeldahl nitrogen*	Sulphate
Nitrite	Maximum lake depth
Soluble phosphorus	
Potassium	
Silica	
Iron	
*Bosmina longirostris**	*Eubosmina longispina*
*Daphnia ambigua**	
*Daphnia galeata mendotae**	
*Daphnia longiremis**	
*Daphnia retrocurva**	
Diaphanosoma sp.*	
Eubosmina tubicen	
*Holopedium gibberum**	
*Leptodora kindti**	
Diaptomus reighardi	
*Epischura lacustris**	
Leptodiaptomus minutus	
*Skistodiaptomus oregonensis**	
*Diacyclops thomasi**	
*Mesocyclops edax**	
*Tropocyclops prasinus**	

Discussion

Significant increases in pH, alkalinity, and zooplankton species richness indicate that water quality of lakes in the Sudbury area has improved in the past decade, although many of the study lakes are still highly acidic. Keller and Yan (1991) reached a similar conclusion based on analyses of fewer lakes. Our conclusions regarding species richness are confounded to some extent, as species richness did not change equally in lakes from Keller's (1981) and Sprules' (1975) datasets. Whether this was the result of differences in sampling protocol, time elapsed since the original survey, differences in chemical status (such as metal concentrations or degree of damage sustained in the 1970's, both of which are related to distance from Sudbury), or proximity to a source of colonizing species remains to be determined

TABLE 5. Frequencies of occurrence of the zooplankton taxa used in the PCA of Sudbury area lakes, by lake pH. Data for all three time periods are combined.

Taxon	Percentage of lakes with taxon present		
	pH < 5.0 (N = 86)	pH 5.0–5.9 (N = 62)	pH ≥ 6.0 (N = 30)
Bosmina longirostris	60.5	85.5	96.7
Chydorus sphaericus	19.8	17.8	23.3
Daphnia ambigua	7.0	37.1	16.7
Daphnia catawba	24.4	21.0	10.0
Daphnia galeata mendotae	9.3	12.9	63.3
Daphnia longiremis	7.0	6.5	30.0
Daphnia pulex	8.1	12.9	10.0
Daphnia retrocurva	8.1	19.4	53.3
Diaphanosoma sp.	27.9	66.1	93.3
Eubosmina longispina	27.9	25.8	13.3
Eubosmina tubicen	10.5	56.5	23.3
Holopedium gibberum	54.7	83.9	86.7
Leptodora kindti	2.3	12.9	46.7
Polyphemus pediculus	25.6	21.0	6.7
Diaptomus reighardi	3.5	17.7	33.3
Leptodiaptomus minutus	84.9	90.3	93.3
Skistodiaptomus oregonensis	2.3	17.7	73.3
Epischura lacustris	2.3	6.5	60.0
Diacyclops thomasi	15.1	40.3	60.0
Mesocyclops edax	25.6	69.4	96.7
Tropocyclops prasinus	5.8	29.0	63.3

TABLE 6. Abundances of the zooplankton taxa used in the PCA of Sudbury area lakes, by lake pH. Data for all three time periods are combined.

Taxon	Mean (±SD) abundance/m^3		
	pH < 5.0 (N = 86)	pH 5.0–5.9 (N = 62)	pH ≥ 6.0 (N = 30)
Bosmina longirostris	1521.0 ± 3154.17	4294.8 ± 13644.82	2731.1 ± 4629.49
Chydorus sphaericus	19.4 ± 101.55	5.9 ± 22.58	36.0 ± 138.33
Daphnia ambigua	10.5 ± 73.75	93.4 ± 269.59	13.6 ± 44.34
Daphnia catawba	103.6 ± 593.18	79.6 ± 246.33	846.5 ± 4678.22
Daphnia galeata mendotae	1.8 ± 7.06	62.3 ± 312.78	544.0 ± 1268.58
Daphnia longiremis	1.8 ± 8.94	20.5 ± 154.15	124.4 ± 313.21
Daphnia pulex	307.0 ± 1558.14	54.5 ± 286.28	3.3 ± 12.34
Daphnia retrocurva	3.5 ± 16.66	23.3 ± 89.06	850.8 ± 2233.36
Diaphanosoma sp.	1349.7 ± 10338.38	1348.4 ± 4336.31	2248.47 ± 2653.22
Eubosmina longispina	265.1 ± 1002.49	95.9 ± 296.62	6.6 ± 27.63
Eubosmina tubicen	19.7 ± 103.48	1216.6 ± 4252.95	306.8 ± 1289.42
Holopedium gibberum	1013.1 ± 2636.82	1480.5 ± 2509.18	822.3 ± 1777.65
Leptodora kindti	0.2 ± 2.16	8.8 ± 34.28	39.6 ± 85.03
Polyphemus pediculus	24.9 ± 77.65	18.1 ± 48.94	0.7 ± 2.55
Diaptomus reighardi	0.02 ± 0.10	146.8 ± 1008.40	1039.9 ± 5623.91
Leptodiaptomus minutus	7224.9 ± 10888.01	6215.1 ± 11714.48	6393.3 ± 17639.12
Skistodiaptomus oregonensis	0.7 ± 5.43	72.5 ± 292.23	984.6 ± 1953.99
Epischura lacustris	0.04 ± 0.31	2.6 ± 14.09	163.5 ± 307.75
Diacyclops thomasi	48.0 ± 285.49	560.3 ± 1517.48	1400.2 ± 3229.77
Mesocyclops edax	94.8 ± 430.46	417.1 ± 849.27	2389.9 ± 5366.01
Tropocyclops prasinus	347.1 ± 3176.46	196.7 ± 676.43	1992.8 ± 7814.51

and will be addressed by W.G. Sprules et al. (in preparation).

Trajectories of community change in recovering acid lakes vary substantially, especially in the early stages of recovery from highly acidic (pH < 5.0) to moderately acidic pH (5.0–5.9). Studies of community assembly (e.g., Robinson and Dickerson 1987; Robinson and Edgemon 1988; Drake 1991) have demonstrated the importance of invasion sequence and invasion rate in determining the composition of communities derived from the same species pool. The stochastic nature of species invasions is probably responsible for the observed high variability in community trajectories in lakes at early stages of recovery with low species richness. The convergence of trajectories in lakes recovered to pH ≥ 6.0 suggests that given sufficient time, zooplankton community structure of

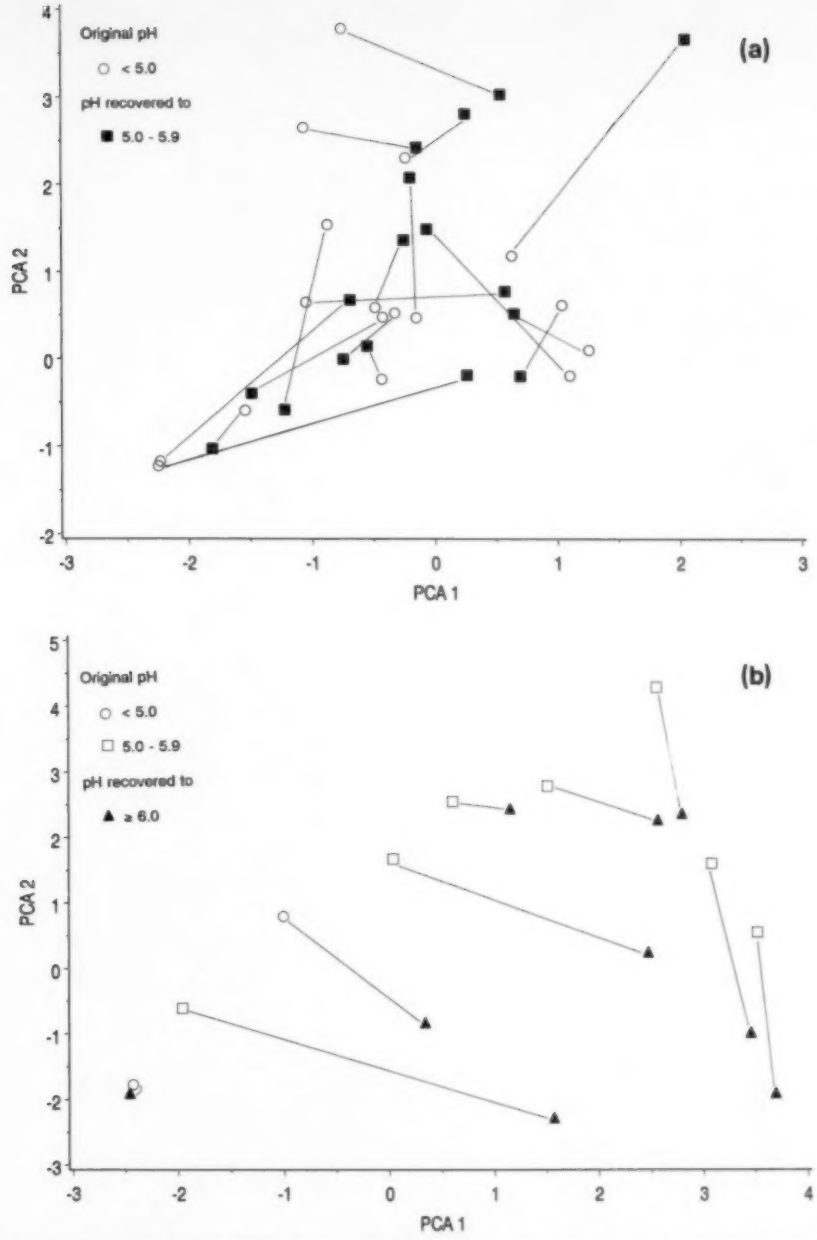

FIG. 5. Trajectories of community change followed by lakes that recovered from (a) pH < 5.0 to pH 5.0–5.9 and (b) pH < 6.0 to pH ≥ 6.0.

recovering lakes may approach that of circumneutral lakes. Two major features of these lakes are the higher abundance of zooplankton relative to more acidic lakes and the presence of acid-sensitive species (Fig. 4; Tables 4–6).

Zooplankton community recovery was slower than chemical recovery, and most lakes incorporated a substantial "lag time" before zooplankton communities resembled those of the pH category to which the lake had chemically recovered. "Full" recovery of the zooplankton community (i.e., attainment of PCA scores on axis 1 similar to those of lakes with pH ≥ 6.0 in the original surveys) had not occurred in most lakes despite a decade of reduced emissions. Likewise, in Bowland Lake, a limed lake in the Sudbury area, recovery of the crustacean zooplankton community was not complete after 4 yr at pH > 6.0 (Keller et al. 1992c). The degree and rate of biological recovery possible are probably related to the initial degree of environmental degradation, extent of water quality improvements, time elapsed since the water quality improvements, and the dispersal capabilities of potential colonizers, including resting eggs surviving in the

sediments (Keller and Yan 1991). Observed recolonization times for crustacean zooplankton in neutralized lakes in the Sudbury area range from 2 to 12 yr (Keller et al. 1992a, 1992b). It is likely that natural biological recovery in the study lakes would take longer than in neutralized lakes because water chemistry improvements are slower, although ultimately these improvements are not necessarily of lesser extent (e.g., Gunn et al. 1988). Keller et al. (1992b) have suggested that the effect of a change in acid input could take close to a decade to be fully reflected in lake water chemistry under average hydraulic retention times of 3 yr. Thus, zooplankton community recovery in some of the study lakes may take more than a decade. Based on the results of the present survey, further improvements in the biotic status of the Sudbury area lakes should eventually be observed if current emission standards are sustained or improved. The results also suggest that water quality improvements anticipated to result from ongoing emission control programs in Ontario and the United States should lead to general recovery of zooplankton communities in many currently acid-stressed lakes in eastern North America.

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Structure and Dynamics of Photosynthetic Picoplankton across the Saltwater Transition Zone of the St. Lawrence River

Normand Bertrand and Warwick F. Vincent[1]

Département de biologie et Centre d'études nordiques, Université Laval, Ste-Foy, QC G1K 7P4, Canada

Bertrand, N., and W.F. Vincent. 1994. Structure and dynamics of photosynthetic picoplankton across the saltwater transition zone of the St. Lawrence River. Can. J. Fish. Aquat. Sci. 51: 161–171.

Changes in the biomass, community structure, and activity of photosynthetic picoplankton (PP) were measured across the turbid, freshwater–saltwater transition zone (TZ) of the St. Lawrence River. The <2 μm fraction of total Chl *a* dropped from 20–30% in mid-May to 15% in late June. Photosynthesis by the <2.0 μm fraction in May surface waters contributed 6–38% of the total primary production. Picoplankton dropped from 8.4×10^6 (freshwater zone, FZ) to 3.7×10^6 cells·L^{-1} (TZ) in mid-May and from 17×10^6 (FZ) to 5.8×10^6 cells·L^{-1} (TZ) in late June. Results implied that the picoplankton were subject to increased losses (e.g., by protozoan grazing) in the TZ. Phycoerythrin-rich cyanobacteria (PEC) dominated the PP counts in mid-May, with phycocyanin-rich forms (PCC) contributing 4–13% of the cell concentrations. Six weeks later the PP community had shifted completely to PCC dominance (60–69% of total counts). In late summer, PP contributed 6–56% of the planktonic Chl *a* in the St. Lawrence River system. There were large variations in the PEC/PCC ratio and the proportion of eukaryotic PP along certain reaches of the river. These observations underscore the spatially and temporally dynamic character of PP communities in the river–estuary environment.

Nous avons mesuré les modifications dans la biomasse, la structure des communautés et l'activité du picoplancton photosynthétique (PP) dans la zone de transition de l'eau douce à l'eau salée dans le Saint-Laurent. La fraction < 2 μm de Chl *a* totale a chuté, passant de 20–30 % à la mi-mai à 15 % à la fin juin. La photosynthèse effectuée par la fraction < 2,0 μm dans les eaux superficielles en mai représentait 6–38 % de la production primaire totale. La concentration de picoplancton a chuté, a passant de $8{,}4 \times 10^6$ (eau douce) à $3{,}7 \times 10^6$ cellules·L^{-1} (zone de transition) à la mi-mai et de 17×10^6 (eau douce) à $5{,}8 \times 10^6$ cellules·L^{-1} (zone de transition) à la fin juin. Les résultats semblent indiquer que le picoplancton subissait des pertes croissantes (p. ex. broutage par les protozoaires) dans la zone de transition. Les cyanobactéries riches de phycoérythrine (PEC) dominaient les effectifs de PP à la mi-mai, tandis que les formes riches en phycocyanine (PCC) représentaient 4–13 % des concentrations de cellules. Six semaines plus tard, la communauté de PP avait complètement changé, passant à une dominance des PCC (60–69 %) de l'effectif total). À la fin de l'été, le PP représentait 6–56 % de la Chl *a* planctonique dans le système du Saint-Laurent. On observait de fortes variations du rapport PEC/PCC et de la proportion du PP eucaryote le long de certains tronçons du fleuve. Ces observations soulignent le caractère dynamique tant spatialement que temporellement des communautés de PP dans un milieu estuarien.

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Photosynthetic picoplankton (PP) have become the focus of increasing research interest in ocean and lake ecosystems (e.g., Stockner and Antia 1986; Sherr and Sherr 1991), but little is known about their ecology in rivers and associated estuaries. These environments are regions of sharp gradients in physical and chemical properties, and they often support large standing stocks of phytoplankton as well as secondary producers (e.g., Barclay and Knight 1981; Jackson et al. 1987; Servais and Garnier 1990; Alpine and Cloern 1992).

Although PP are commonly thought of as characteristic of oligotrophic waters (e.g., Fahnenstiel et al. 1986; Weisse 1988; Pick 1991), there is recent evidence that *Synechococcus* may sometimes bloom in productive estuarine and lake environments (Falkenhayn and Haas 1990; Maeda et al. 1992; Affronti and Marshall 1993). Picoplankton have a better light-capturing ability than other phytoplankton groups (Kirk 1986), which might favour their success in turbid rivers and estuaries.

Natural PP communities encompass a broad range of spectral absorbance characteristics: eukaryotes (EUK) contain Chl *a* and either Chl *b* or Chl *c*, with maximal absorbance in the blue waveband (400–500 nm); phycoerythrin-rich cyanobacteria (PEC) absorb maximally in the green (500 nm), and phycocyanin-rich cyanobacteria (PCC) absorb maximally in the red (615 nm). Cellular phycoerythrin concentration is also known to respond to changes in white light intensity (e.g., Wyman and Fay 1986a) as well as spectral composition of the irradiance (e.g., Wyman and Fay 1986b). Both spectral irradiance and total irradiance are likely to shift along a turbidity gradient and thereby influence the pigment characteristics of the PP.

The aim of the present study was to evaluate the structure and dynamics of the PP communities in the St. Lawrence

[1]Author for correspondence.

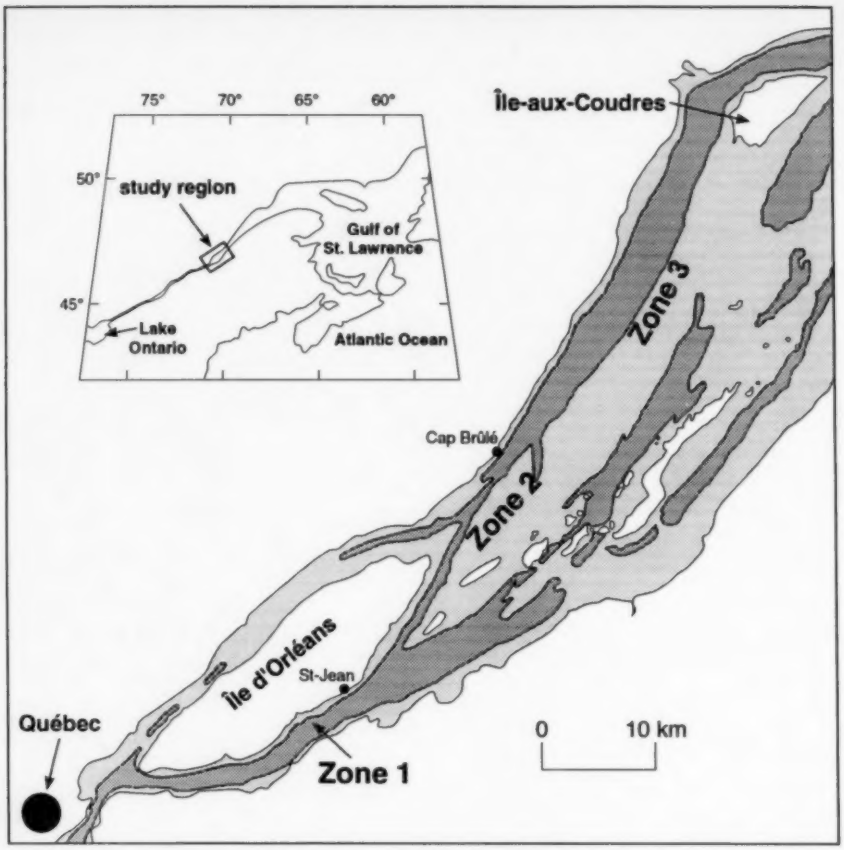

FIG. 1. Study area and location of the study zones. Light shading marks the regions less than 10 m depth and the dark shading marks the regions deeper than 10 m.

River system. We examined the PP contribution to the total algal community in the downstream, freshwater reach of the St. Lawrence River and into and across the estuarine transition zone (TZ). Our most intensive sampling period was timed during spring – early summer, a period of rapid seasonal change in the riverine environment. At this time of year the TZ is a major nursery for larval fish such as Atlantic tomcod (*Microgadus tomcod*) and rainbow smelt (*Osmerus mordax*) (Dodson et al 1989; Laprise and Dodson 1989), and the primary food chain processes are therefore of special interest. The TZ is a highly turbid region and has been referred to as the maximum turbidity zone (Lucotte and d'Anglejan 1986) of the St. Lawrence estuary. We hypothesised that the turbidity gradient across this freshwater–saltwater transition would have a major influence on PP biomass, productivity, and pigment structure.

Description of the Transition Zone

The TZ is located between 50 and 90 km downstream of Québec City and is defined by the transition from freshwater to 10‰ salt water (d'Anglejan and Smith 1973; Kranck 1979). It is a region of strong tidal currents, estuarine recirculation, and sediment resuspension (Cardinal and Bérard-Thérriault 1976; Kranck 1979) with turbidity values up to 115 NTU (Lucotte and d'Anglejan 1986). The sediment is derived from large nearby marshes as well as by flocculation of particles entering the system from upstream (Kranck 1979).

Previous authors have noted a large decrease in phytoplankton cell counts as well as Chl *a* within the TZ. Cardinal and Bérard-Thérriault (1976) recorded an order of magnitude drop in cell concentrations between Île d'Orléans and Île-aux-Coudres (Fig. 1), although they also noted that a large cell count (in absolute terms) continued to persist in the TZ. Painchaud et al. (1990) recorded a decrease from 2.9 to 1.0 μg Chl $a \cdot L^{-1}$ over the same distance in the late summer. This decline in photosynthetic biomass has been attributed to decreases in underwater light availability, coupled with the osmotic stress associated with rising salinities (Thérriault et al. 1990).

Materials and Methods

Two sampling cruises were undertaken, from 10 to 14 May 1991 and from 27 June to 1 July 1991. During the first cruise, 12 stations were sampled in the upper St. Lawrence Estuary (Fig. 1): four stations in the lower freshwater (but tidal) zone (FZ) approximately 30 km downstream of Québec City (Zone 1), four stations in the frontal region of increased turbidity with surface salinities in the range 0.7–2‰ (Zone 2), and four stations 30 km further downstream with surface water salinities in the range 4–8‰ (Zone 3). The four stations

in Zone 1 were within a 2-km reach of the main channel centered at the position marked by the arrow in Fig. 1. The four stations in Zones 2 and 3 were also in the main channel (marked by dark shading in Fig. 1) and were located within 8-km reaches. Each zone was sampled over a 24-h period, twice at low tide and twice at high tide.

Zone 1 and the Zone 2 frontal region were more intensively studied in the second cruise to obtain better temporal resolution of the tidal water masses. A fixed station was occupied in each zone and sampled at 3- to 4-h intervals over three tidal cycles. The freshwater station was located approximately 500 m off St. Jean (Île d'Orléans) and the TZ station was located within 1 km of Cap Brûlé (north shore).

A third period of sampling was undertaken in late summer (16–17 September 1991) to examine the PP gradients down the entire St. Lawrence River ecosystem. Samples were taken at 0.5 m depth with a Van Dorn bottle, from piers extending into the flowing river at 12 sites between Kingston (Ontario) and St. Siméon (Québec), 770 km downstream. The sample at Lac St. Pierre was obtained by boat 500 m from the shore at Louiseville. The samples were fractionated as described below. Unusually high Chl *a* values at the northern site (St. Anne) of the TZ led us to resample this region by boat 2 wk later (31 September). The original Zone 1 and 2 sites were also resampled at this time.

At each sampling time during the two cruises, water was obtained from near the surface (0.5 m) and near the bottom (17 m, which was at least 3 m above the sediments) with a 5-L GO-FLOW sampling bottle. Temperature and salinities were obtained with Sea Bird CTD probe model Sealogger SBE-19. Quantum scalar irradiance was measured with a Biospherical Instrument Co. 4π QSP-160 sensor connected to a QSP-170B integrating meter. Turbidity was assessed by dry weight analysis of the seston filtered onto preweighed GF/F glass fiber filters.

Samples for nutrient analysis were prefiltered through GF/F filters, stored frozen, and later analysed on a Alpkem model RFA-300 autoanalyser. Nitrate was measured by diazotization after cadmium reduction to nitrate (American Public Health Association 1976), dissolved reactive phosphorus (DRP) by the method of Whitledge et al. (1981), and silicate, after repolymerization at room temperature, by the method of Truesdale and Smith (1975). The limits of detection were 0.2 μmol P or Si·L^{-1} and 0.02 μmol N·L^{-1}.

Water samples for picoplankton analysis were screened through 200- and then 20-μm Nitex filters into 60-mL Nalgene amber bottles and immediately preserved with 0.2% (final concentration) paraformaldehyde (Hall and Vincent 1990). We evaluated two prefiltration protocols for the PP sample preparation. Test samples from the TZ were prefiltered through either a 2-μm Nuclepore filter or a 20-μm Nitex screen. In samples from both the TZ and FZ, the 2-μm prefiltration resulted in a significant loss of counts. The 2-μm prefiltration gave a mean of 17% lower total counts for five FZ samples and 67% lower counts for five TZ samples. The severe reduction in counts was observed for both the cell aggregates as well as single cells and probably resulted from the rapid blockage of the Nuclepore membrane. We therefore selected a 20-μm prefiltration for all samples.

The samples were stored at 4°C for up to 2 wk and then filtered onto black Nuclepore 0.2-μm membranes. These were mounted on slides with immersion oil and a coverslip, sealed, and stored frozen at −20°C. The slides were then examined 1–3 mo later by epifluorescence at 1000× magnification using a Zeiss Axiovert 10 microscope fitted with a Zeiss Plan-Neofluor 100×/1.30 objective. Preservation tests reported in Hall (1991) with this protocol indicate that there should have been no significant degradation of picoplankton counts over this period of storage.

Each field was first examined under green light using Zeiss filter set 15 with a 546/12-nm exciter filter, a 850-nm beam splitter, and 590 barrier filter. The same field was then examinated under blue light using Zeiss filter set 05 (blue); this consists of a 450- to 490-nm exciter filter, a 510-nm beam splitter, and a 520 barrier filter. PCC were identifed as those cells which fluoresced orange–red under green excitation and very pale red under blue excitation. PEC were distinguished by their strong orange fluorescence under green light and yellow fluorescence under blue light excitation. The chlorophyll-dominated cells (probably EUK) were distinguished by their strong red fluorescence under blue light (Tsuji et al. 1986). The picoplankton community was separated into two additional groups: single cells and cell aggregates (colonies or clumps of two or more cells). A total of at least 400 cells were counted in each sample. Cell size was measured for each picoplankton category using an eyepiece micrometer calibrated against a stage micrometer.

Subsamples of water for Chl *a* fractionation were prefiltered through either a Nitex 200-μm screen (total fraction), a Nitex 20-μm screen (<20 μm fraction), or a Nuclepore 2-μm filter (picoplancton, <2 μm fraction) and then filtered onto 25-mm Whatman GF/F filters. Care was taken to rinse each filter with GF/F-filtered sample water during and at the end of filtration to minimize filter blockage effects. These filters were stored frozen and subsequently ground in 90% acetone with a Teflon tissue grinder. The extract was cleared by centrifugation and assayed by fluorometry (Shimadzu spectrofluorometer model RF5000U) before and after acidification (Strickland and Parsons 1972).

Photosynthetic rates were measured by the ^{14}C method as described in Strickland and Parsons (1972). Each sample was dispensed immediately after collection into 70-mL Corning polycarbonate bottles and inoculated with 5.6×10^8 Bq of $NaH^{14}CO_3$. The bottles were incubated in a water bath set to surface water temperatures and under a photon fluence rate of 180 μmol photons·m^{-2}·s^{-1} provided by a 250-W Optimarc high pressure sodium lamp. At the end of a 2-h incubation the samples were fractionated as for Chl *a* and the filters then immediately frozen. The filters were subsequently acidified for 5 min in an atmosphere of HCl and were each placed in a scintillation vial containing 10 mL of Cytoscint. The ^{14}C activity was measured in a LKB 1219 RackBeta liquid scintillation counter. Dissolved inorganic carbon (DIC) was measured by pH and potentiometric titration (Wetzel and Likens 1991) of 50-mL subsamples. These analyses were completed within 10 min of sample collection.

Results

Physical and Chemical Environment

During the mid-May cruise the mean water temperature dropped slightly between zones, from 10.3°C in Zone 1 to 7.2°C in Zone 3 (17 m). Salinity increased over this region from 0.09 (fresh) to 9.95‰ (Table 1). For all of the sur-

TABLE 1. Physical and chemical data for the two cruises. Each value is the mean (±SE) for four samples during the first cruise, for 13 samples for each depth in Zone 1 during the second cruise, and for three or four samples at each tidal state in Zone 2 during the second cruise. Tidal state: H = high, F = flood, L = low, E = ebb, and M = mean of low and high tide.

Zone	Depth (m)	Tidal state	Temperature (°C)	Salinity (‰)	Seston ($mg \cdot L^{-1}$)	Nutrients ($\mu mol \cdot L^{-1}$)		
						NO_3^-	DRP	SiO_2
Cruise 1								
1	0.5	M	10.3	0.1	10.6	18.1	0.12	74.7
			(0.1)	(0.0)	(0.2)	(0.1)	(0.0)	(1.6)
	17		10.9	0.1	10.1	17.8	0.11	74.2
			(0.1)	(0.0)	(0.2)	(0.7)	(0.0)	(1.0)
2	0.5	M	10.1	0.8	61.2	14.8	0.27	91.0
			(0.1)	(0.3)	(0.4)	(0.8)	(0.0)	(4.0)
	17		9.4	2.6	106.1	13.8	0.36	86.6
			(0.5)	(1.1)	(23.3)	(0.7)	(0.7)	(6.4)
3	0.5	M	9.2	5.0	54.0	13.5	0.42	80.9
			(0.3)	(0.4)	(3.3)	(0.6)	(0.0)	(2.0)
	17		7.2	10.0	200.0	11.2	0.56	68.9
			(0.3)	(0.7)	(61.7)	(1.2)	(0.1)	(8.1)
Cruise 2								
1	0.5	M	21.3	0.1	6.7	13.0	0.19	18.7
			(0.1)	(0.0)	(0.8)	(0.6)	(0.0)	(0.9)
	17		21.3	0.1	6.9	12.6	0.17	19.4
			(0.1)	(0.0)	(0.8)	(0.6)	(0.0)	(0.8)
2	0.5	F	19.3	3.4	128.4	25.1	0.55	17.6
			(0.1)	(0.4)	(28.0)	(0.9)	(0.7)	(1.6)
	17		19.2	3.7	213.6	23.7	0.59	17.7
			(0.2)	(0.3)	(32.8)	(3.6)	(0.1)	(1.4)
	0.5	H	17.6	6.2	28.0	19.6	0.48	18.0
			(0.6)	(0.9)	(4.2)	(2.4)	(0.5)	(1.1)
	17		15.8	9.6	65.9	21.5	0.60	19.9
			(0.7)	(1.1)	(18.2)	(3.6)	(0.1)	(1.4)
	0.5	E	17.9	5.5	33.9	20.9	0.53	20.8
			(0.1)	(0.4)	(5.0)	(3.7)	(0.8)	(1.2)
	17		17.2	7.23	60.3	22.8	0.52	20.5
			(0.1)	(0.2)	(22.5)	(1.3)	(0.6)	(2.7)
	0.5	L	21.2	0.4	66.2	18.2	0.39	10.9
			(0.2)	(0.1)	(17.2)	(1.5)	(0.1)	(0.4)
	17		21.0	0.6	344.1	21.9	0.49	10.6
			(0.1)	(0.2)	(117.5)	(1.2)	(0.1)	(1.0)

face and bottom water data obtained during the first cruise, there was a close inverse correlation ($r = -0.98$, $p < 0.001$) between temperature and salinity. The temperature and salinity profiles indicated that in Zone 1 the water column was always well mixed, while slightly stratified in Zone 2 and more strongly stratified in Zone 3.

Temperatures were up to 11°C higher in the second cruise (June–July), ranging from 21.3°C in freshwater Zone 1 to 15.8°C at high tide in Zone 2. The salinity bracketed a similar range to the Zone 1–3 values measured in the first cruise. There was no evidence of density stratification in Zone 1, but in Zone 2 the extent of stratification varied over the tidal cycle. The water column was weakly stratified at low and ebbing tide but much more strongly stratified at high and flooding tide. The high tide conditions in Zone 2 resembled the Zone 3 water column sampled in the first cruise and reflected the upstream tidal advection of water from further down the estuary.

The turbidity of the surface and bottom waters varied greatly between zones and between the two cruises. The latter effect was especially apparent for freshwater Zone 1 where the mean seston concentration dropped by 60% between cruises 1 and 2. This effect reflected the major decrease in freshwater discharge, from 16 400 $m^3 \cdot s^{-1}$ in May to 10 400 $m^3 \cdot s^{-1}$ in June (Environnement Québec, unpublished daily averages for 10 May 1991 and 27 June 1991).

In both cruises, there was a sharp increase in seston between Zones 1 and 2. Surface water samples in Zone 3 contained slightly lower seston concentration, confirming that Zone 2 corresponded to the maximum turbidity zone as described by Lucotte and d'Anglejan (1986). During the tidal measurements in the second cruise, highest turbidities in Zone 2 were observed at flood tide and the lowest at high tide (Table 1) which is also consistent with the observations of Lucotte and d'Anglejan (1986).

In the first cruise the depth of the 1% PAR level averaged 2.9 m in Zone 1, 0.9 m in Zone 2, and 1.2 m in Zone 3. There was a large increase in water column transparency between the two cruises, especially in the FZ. The 1% light level in the second cruise averaged 4.2 m in Zone 1 and ranged from 0.9 to 2.3 m in Zone 2.

There were no major differences in nitrate or DRP concentration between mid-May and late June, but silicate levels dropped substantially over this period (Table 1). In both cruises, there was a significant rise in DRP from Zone 1 to 2,

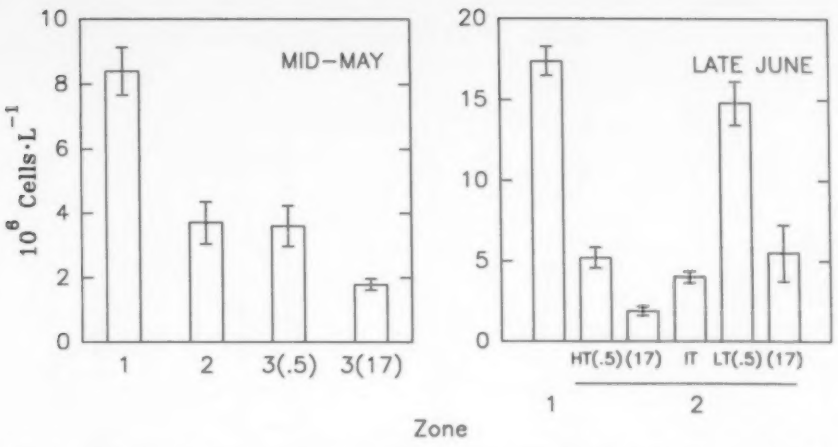

FIG. 2. Total picoplankton concentrations across the TZ. HT: high tide; IT: intermediate tide; LT: low tide; (.5) and (17): 0.5 and 17 m.

and in the second cruise, there was a significant rise in nitrate concentrations across this transition.

Abundance and Distribution of Picoplankton

There were large variations in all categories of picoplankton over time (tidal state and season) and space (zone and depth). The cell concentration of total picoplankton during the first cruise averaged $8.4 \times 10^6 \cdot L^{-1}$ in the freshwater Zone 1 and dropped to $3.7 \times 10^6 \cdot L^{-1}$ in Zone 2 (Fig. 2). There were no depth-dependent variations in picoplankton cell counts in Zones 1 and 2, but in Zone 3 the bottom concentrations were twofold lower than at 0.5 m.

The picoplankton cell counts in the FZ approximately doubled between cruises to an average of $17.4 \times 10^6 \cdot L^{-1}$ in cruise 2. The detailed temporal sampling in the second cruise showed that there was a strong tidal influence on cell concentration in the TZ, but not in the FZ. During high and intermediate tides the total TZ picoplankton counts were well below those in Zone 1, as observed in the first cruise. At low tide, however, there was no significant difference between the counts at 0.5 m for the TZ and Zone 1.

As for the first cruise, there was no evidence of stratification of picoplankton in the FZ. However, there was often a significant difference ($p < 0.05$) between the 0.5- and 17-m total cell counts in the TZ, even at low tide when the temperature and salinity profiles showed negligible variation with depth.

Picoplankton Community Structure

There was a major shift in community structure between cruises, while relatively small changes were observed between zones (Fig. 3). During the first cruise the total PP count in all zones was dominated by PEC (Fig. 3). In the FZ, PEC colonies averaged 60% of the total picoplankton count, while free-living PEC cells contributed an additional 12%. In Zones 2 and 3 the PEC concentrations (colonial plus single cells) contributed 48% of the total picoplankton count. The EUK contributed 27% of the cell counts in all three zones. For the single cell components (Fig. 3), EUK cells were dominant or codominant.

The picoplankton community dominance changed completely in the second cruise. The PCC cells which had made a very small contribution (8%) in mid-May now dominated the total community counts. PCC cells contributed 66% of the FZ community and 60% of the TZ community. This effect was primarily the result of a major increase in PCC cell concentrations; PEC and EUK concentrations changed little between the cruises.

The magnitude of these changes in community pigment structure can be further seen by a comparison of the PEC/total cyanobacteria and EUK/total picoplankton ratios (Table 2). The former ratio did not change significantly between zones, with the exception of a slight and significant drop in Zone 3 at 17 m. However, between mid-May and June, both the PEC/total cyanobacteria and EUK/total picoplankton ratios dropped by a factor of 2.

Colonial versus Single Cells

Cell pairs or larger aggregates of picoplankton made a sizable contribution to the total cell counts in most samples. In the first cruise, 66% of the PP were in colonial form in Zone 1 and 50% in Zones 2 and 3. This proportion dropped in the second cruise to 27% in Zone 1 and 25% in Zone 2.

On average, 47–76% of the aggregates were pairs of cells. These cell pairs were dominated by PCC during the first cruise, but by late June, there was a large and significant ($p < 0.05$) increase in the percentage of PEC cell pairs. In the second cruise the colonies of both groups of cyanobacteria were dominated by cell pairs. The PCC cells pairs averaged 42% (FZ) and 25% (Zones 2 and 3) of the total PCC counts in the first cruise, dropping to 12% in the second cruise. The PEC cell pairs amounted to 16–18 % of the total PEC count in both cruises. The larger aggregates of cyanobacteria contained 4–20 cells; however, the aggregates of EUK were rarely composed of more than two cells.

The picoplankton in all groups averaged cross-sectional diameters in the range 1.1–1.5 μm and biovolumes in the range 0.7–1.8 μm^3. The PEC colonial cells and the EUK cells were significantly larger than the cells in the other picoplankton groups (Table 3).

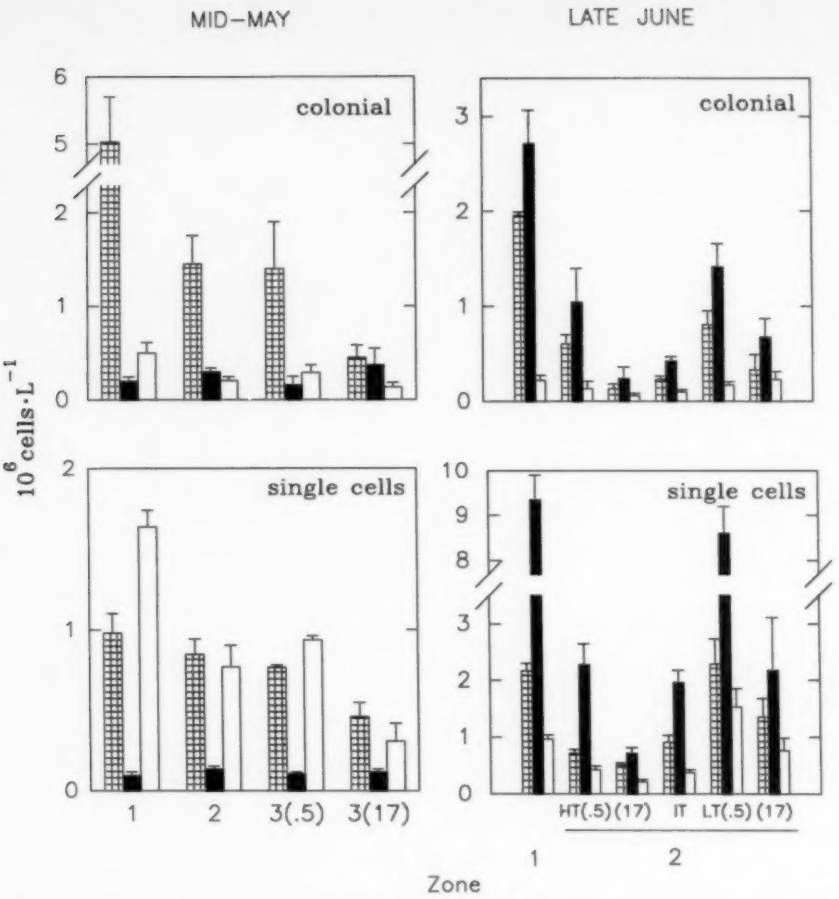

FIG. 3. Changes in PP community structure. Each value is the mean concentration for each PP group. Cross-hatched: PEC; solid: PCC; open: EUK.

TABLE 2. PEC/total cyanobacteria and EUK/total picoplankton ratios for the two cruises. Both colonial and single forms were included. TCC: total cyanobacteria count; TPC: total picoplankton count; n = number of samples. Tidal state: M = mean of high and low tide, H = high tide, L = low tide, and I = intermediate tide.

Zone	Depth (m)	n	Tidal state	PEC/TCC (%)	EUK/TPC (%)
Cruise 1					
1	0.5 and 17	8	M	95.2 (0.8)	26.4 (2.5)
2	0.5 and 17	8	M	81.9 (4.0)	26.0 (2.0)
3	0.5	4	M	89.6 (2.0)	32.6 (2.2)
	17	4		65.5 (6.7)	25.7 (7.7)
Cruise 2					
1	0.5 and 17	26	M	25.8 (1.0)	7.5 (0.5)
2	0.5	3	H	29.8 (5.3)	10.6 (2.5)
	17	3	H	40.8 (2.8)	20.2 (3.8)
	0.5 and 17	12	I	32.9 (2.4)	16.1 (0.8)
	0.5	4	L	23.2 (1.2)	14.2 (1.5)
	17	4	L	39.3 (3.0)	21.4 (3.4)

PP Contribution to Total Chl *a*

Chl *a* biomass in the picoplankton fraction remained similar in the two cruises. The percent contribution of PP to total Chl *a* dropped significantiy between cruises in the FZ (Fig. 4). During the first cruise, the picoplankton fraction dropped significantly ($p < 0.05$) from 30% of total Chl *a* in

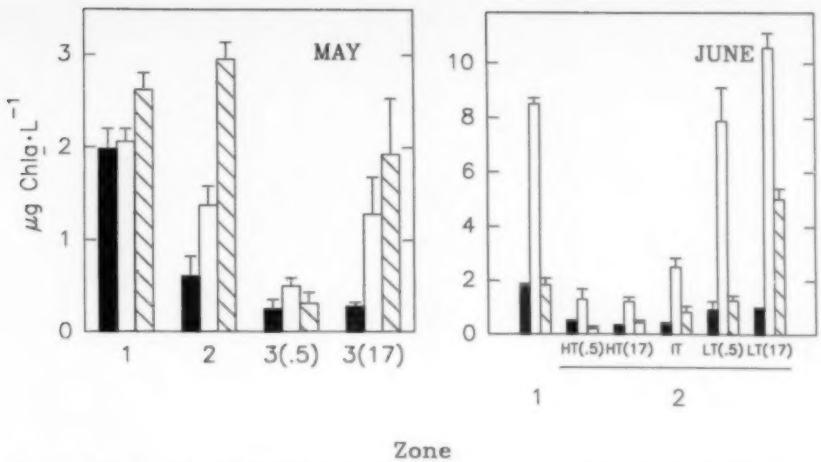

FIG. 4. Distribution of the three Chl *a* fractions across the TZ. Solid: picoplankton; open: nanoplankton; hatched: microplankton.

Zone 1 to 13% in Zone 2. In Zone 3, there was a significant difference between the surface water (22%) and bottom water (10%). By the second cruise the Zone 1 PP had dropped to 15% of total Chl *a* but did not change significantly across the transition into Zone 2. In the first cruise the dominant Chl *a* constituent was the microplankton fraction (20–200 μm), while in the second cruise the nanoplankton fraction (2–20 μm) dominated.

River Survey

The synoptic survey along the full reach of the St. Lawrence River system in late summer showed that picoplankton were always an important component of the total phytoplankton community. There were systematic changes in the pigment characteristics of PP along certain reaches, but not across the TZ (Fig. 5).

Total Chl *a* concentrations remained relatively constant, within the range 1.5–3 $\mu g \cdot L^{-1}$ along more than 500 km of the upstream freshwater section of the river. In the downstream saltwater section, Chl *a* values fell to less than 0.3 $\mu g \cdot L^{-1}$. Turbidity as measured by Secchi depth was maximal in the TZ as expected. However, the Chl *a* concentrations at this site (marked by the broken line in Fig. 5) were unusually high. This sample was obtained from the pier at St. Anne on the left branch of the St. Lawrence River, north of Île d'Orléans. Two weeks later (31 September), we repeated our sampling at this site by boat at a station several hundred metres offshore. At this time the Chl *a* averaged ($n = 3$) 5.5 $\mu g \cdot L^{-1}$ at 0.5 m depth and 8.0 $\mu g \cdot L^{-1}$ at 10 m depth. These values were four to five times higher than in the freshwater section of the river sampled on the same day at the offshore Zone 1 on the southern branch of the St. Lawrence near St. Jean (1.4 μg Chl $a \cdot L^{-1}$). Within Zone 2 at this time the 0.5-m Chl *a* values were 2.4 $\mu g \cdot L^{-1}$ off Cap Tourmente, falling to 0.8 $\mu g \cdot L^{-1}$ off Cap Brûlé. In the full river survey the PP contribution averaged 34% of total Chl *a*, but with considerable variation between sites (SD = 17%). Negligible variation in picoplankton community structure was observed across the saltwater transition, consistent with the results from the two cruises. However, downstream of Montréal there was an abrupt shift from PEC to PCC dominance, followed by a steady rise back towards PEC dominance down the next 400 km of the river system. This latter effect was accompanied by a rise in the percent importance of EUK cells which eventually accounted for 25–56% of the PP counts in the downstream saltwater section. There was a strong inverse correlation ($r = -0.92$, $p < 0.001$) between the percent EUK cells and temperature.

TABLE 3. Mean dimension and biovolume of the St. Lawrence PP.

PP	*n*	Mean dimension (μm)	Mean biovolume (μm^3)
PEC, single	588	1.2	0.9
PEC, colonial	83	1.5	1.8
PCC, single	368	1.1	0.7
PCC, colonial	81	1.2	0.9
EUK	250	1.5	1.8

Picoplankton Photosynthesis

Photosynthesis by the <2.0 μm fraction in the first cruise surface waters ranged from 0.3 to 3.3 $\mu g\ C \cdot L^{-1} \cdot h^{-1}$ and contributed 6–38% of the total primary production as measured in our shipboard incubation system (Fig. 6). There was no evidence of a decline in the physiological state of the PP component in the transition from Zone 1 to 2. The surface water (0.5 m) assimilation numbers (photosynthesis per unit Chl *a*) increased, but not significantly ($p > 0.1$), from Zone 1 to 2 and then dropped significantly ($p < 0.05$) between Zones 2 and 3 (Table 4). The bottom-water (17 m) assimilation numbers did not significantly differ across the three zones.

Discussion

PP occurred throughout the St. Lawrence River system but their contribution to the total planktonic biomass varied seasonally and also spatially. The concentrations measured here, from 10^6 to 10^7 cells$\cdot L^{-1}$, fall within the middle to lower end of the range reported from a variety of marine

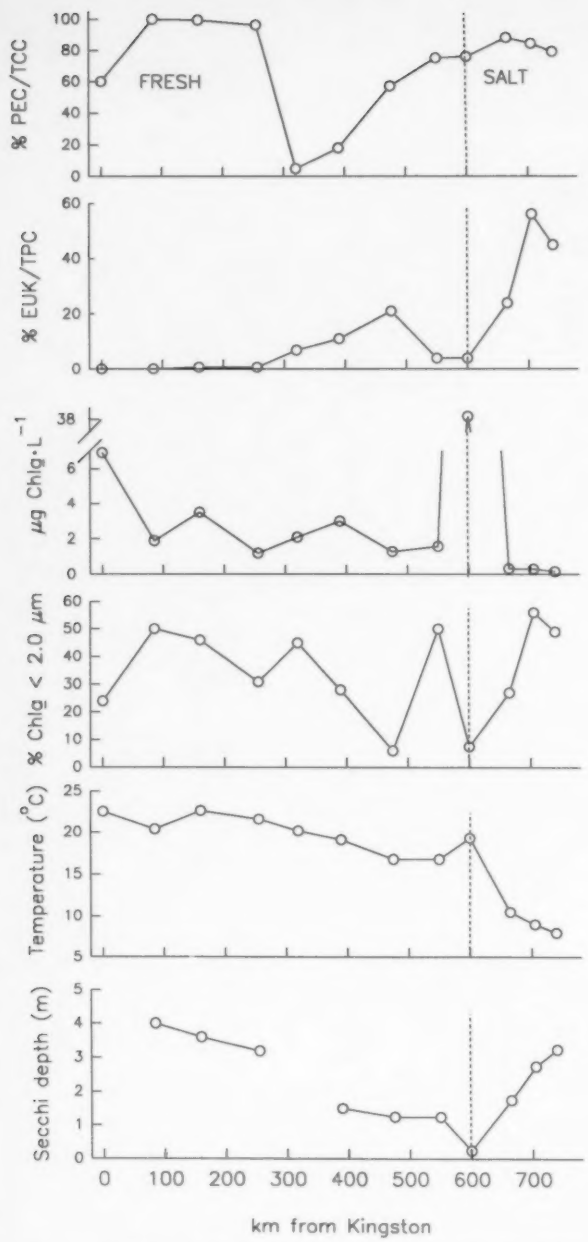

FIG. 5. Distribution of physical and biological properties along the St. Lawrence River system between Kingston and St. Siméon, 16–17 September 1991. The broken line indicates the TZ.

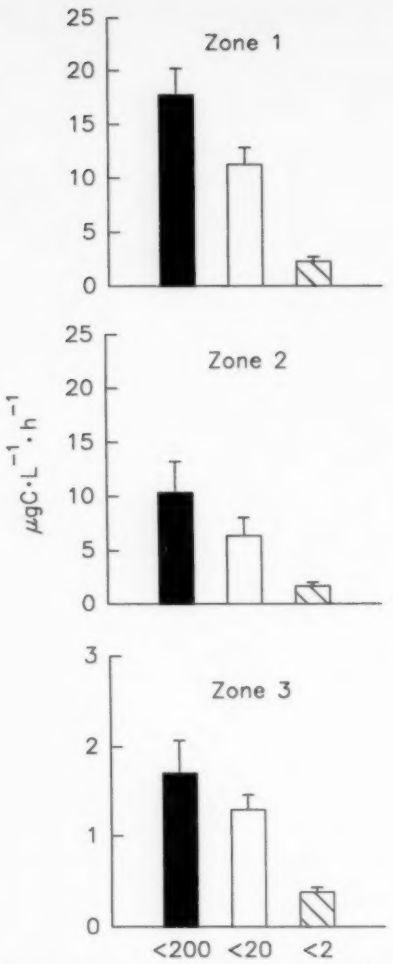

FIG. 6. Primary production for the three fractions (<200, <20, and <2 μm) across the TZ for the first cruise.

and freshwater ecosystems (Waterbury et al. 1979; Johnson and Sieburth 1982; Caron et al. 1985; Fahnenstiel et al. 1986; Fahnenstiel and Carrick 1992). Much higher concentrations, up to 10^9 cells·L^{-1}, have been recorded in certain nutrient-rich environments such as Chesapeake Bay (Affronti and Marshall 1993) and Lake Biwa (Maeda et al. 1992).

Within the TZ of the St. Lawrence River, the PP counts always exceeded 2×10^6 cells·L^{-1}. This highly turbid region has previously been considered a dead zone where rising salinities coupled with the strong attenuation of light would substantially restrict phytoplankton photosynthesis and growth (Thérriault et al. 1990) as well as higher trophic levels (e.g., Bousfield et al. (1975) referred to this region as the "graveyard" of the St. Lawrence River system). Our results, however, indicate that viable cells continue to persist in the TZ, specifically in the Zone 2 frontal region where the seawater influence is first met and where turbidity is maximal. It was only further downstream (Zone 3) that there was a major decrease in Chl *a* (all fractions) and photosynthesis.

Despite the high assimilation numbers, there was a decline in PP cell contribution within the TZ. The phytoplankton biomass remained relatively constant thoughout much of the St. Lawrence system during the late summer sampling, implying a close balance between growth and loss processes. The decline in the TZ may reflect the increased losses that are imposed by zooplankton grazing within this region. Pace et al. (1992) noted that estuaries typically have higher zooplankton than rivers because of their increased residence

times. Recent studies in the St. Lawrence TZ have identified a diverse protozoan community (Lovejoy et al. 1993). These organisms are often observed to have picoplankton within them (C. Lovejoy, Département de biologie, Université Laval, personal communication) and they are a potentially major control on PP abundance (cf. Fahnenstiel et al. 1986).

We were unable to support the hypothesis that the changing underwater light conditions in the TZ cause a shift in PP dominance and pigment structure. The photosynthetic characteristics of the <2 μm fraction did not change significantly across the Zone 1–2 transition, nor did the PEC/cyanobacteria or EUK/total picoplankton ratio. These results imply that either the residence time in this frontal zone is too short for major community-level and physiological adjustments or that there was not the anticipated magnitude of change in the underwater light regime. The TZ contained the highest turbidities within the St. Lawrence River system, and light penetration was minimal in this zone (e.g., Fig. 5). However, the high PAR attenuation may be largely offset by the shallow depth of mixing. The average water column depth in the St. Lawrence at Québec City is 24 m but is 6 m in the Zone 2 region (N. Bertrand and W. Vincent, unpublished data). A major unknown, however, in these environments is the intensity of turbulent mixing and the frequency of exposure of cells to near-surface light conditions. These fluctuations may have a critical influence on PP growth rates and pigmentation, especially in the optically deep environments (sensu Talling 1957) which characterize the entire St. Lawrence River system.

The most striking changes in pigment structure in the TZ occurred temporally rather than spatially. The PEC dominance in May shifted completely to PCC dominance in late June. Our synoptic survey showed that similar changes can occur spatially in the upstream portion of the St. Lawrence River system. The observed temporal shift from PEC to PCC took place at a time of major seasonal change in many aspects of the riverine environment. With the end of the spring snowmelt, discharge dropped 37% and the water temperature increased by 11°C. Silicate dropped fourfold, although nitrate and DRP showed little change. Silicate is not a growth requirement for cyanobacteria, nor for most eukaryotic PP. The observed changes in PP community size and structure are more likely to have been the result of the physical rather than chemical changes in the river environment and specifically in the freshwater section upstream of Zone 1.

Temperature is known to have a wide-ranging influence on PP growth and may have contributed to the doubling of the total picoplankton count between the May and June cruises. For example the distribution of picoplanktonic cyanobacteria in the Southern Ocean directly correlates with temperature, and thus inversely with latitude south (Marchant et al. 1987). Caron et al. (1985) similarly found a correlation between total picoplankton cyanobacteria and temperature in Lake Ontario. In the St. Lawrence River system the proportion of EUK in the picoplankton community seemed to be linked to low temperatures, both temporally (higher EUK/TPC in mid-May) and spatially (negative correlation between EUK/TPC and temperature in the river survey). This relative preference by eukaryotic picoplankton for cold water, or a correlate of such conditions, has been found in a variety of other marine and freshwater environments (Hall and Vincent 1990; Kuosa 1991). However, temperature seems unlikely to have been a major control on pigment structure within the St. Lawrence cyanobacterial community. Many authors have shown the persistence of phycoerythrin-dominated communities throughout the year despite large seasonal variations in ambient water temperature (e.g., Fahnenstiel and Carrick 1992, and references therein).

TABLE 4. Primary production (μg C·μg Chl a^{-1}·h^{-1}) for the PP during the mid-May cruise. Each value is the mean for three or four estimates (SE in parentheses).

Depth (m)	Zone 1	Zone 2	Zone 3
0.5	1.63 (0.7)	3.26 (0.5)	1.05 (0.3)
17	1.22 (0.5)	1.40 (0.7)	1.45 (0.5)

Underwater light regime is likely to have been a more decisive factor influencing the PEC/PCC ratio. Although many authors have identified an effect of light quality (spectral irradiance, e.g., Wyman and Fay 1986b) on pigmentation, the total photon fluence rate may also have an effect. Wyman and Fay (1986a), for example, found that the phycoerythrin/phycocyanin ratio in cultures of cyanobacteria increased with decreasing white light photon flux density. Ohki and Fujita (1992) noted that increases in the PEC/PCC ratio are associated with a major expansion in the cross-sectional diameter, thus light-capturing ability, of the phycobilisome. The high PEC/PCC ratio observed in the St. Lawrence during May may have conferred an improved light-capturing ability during the turbid spring runoff conditions. Affronti and Marshall (1993) similarly ascribed the large increase in the PEC/PCC ratio with depth in Chesapeake Bay to the total irradiance preferences of each group. It is of interest that they also observed PEC dominance in winter, shifting to PCC dominance in the surface waters during summer, consistent with the seasonal trend that we observed in the St. Lawrence estuary.

The large pigment shifts observed here could reflect physiological adjustments in the same population, or they may be the result of environmental selection for specific genotypes. The picoplanktonic genus *Synechococcus* is known to encompass a genetically diverse array of strains and species (Waterbury et al. 1986), and it seems likely that at least some genetic change in the cyanobacterial picoplankton accompanied the major shift in nanoplankton/microplankton observed in the river during the environmentally dynamic spring–summer period. The significant difference in cell size between the PEC and PCC colonial forms provides some indication of genetic differences.

Cell aggregates were an important component of the total picoplankton counts throughout this study, particularly during the first cruise. In the Great Lakes, colonial forms have been similarly identified as a major contributor to the picoplankton community, sometimes accounting for more than 50% of the counts (Fahnenstiel and Carrick 1992). These cellular aggregates may be available to a much wider spectrum of grazers, including crustacean zooplankton, than the very small free-living cells. Cell pairs represented the majority (50–80%) of the aggregates in the St. Lawrence and were small enough to have been included in the <2 μm Chl *a* fraction. Cell pairs have sometimes been used as a measure of "frequency of dividing cells" and thus as

a measure of picoplankton growth rates (e.g., Pick and Bérubé 1992; Affronti and Marshall 1993). The increased frequency of cell pairs for the PCC component (relative to PEC) during the first cruise suggests a faster growth rate by this component, consistent with their eventual dominance of the picoplankton during the second cruise. However, we concur with Fahnenstiel and Carrick (1992) that the exact relationship between cell aggregates and free-living cells warrants much closer attention.

There are a number of sampling and methodological questions which we have not addressed in the present study. A major unknown is the extent of horizontal variability in phytoplankton biomass and community structure at right angles to the direction of flow. On occasion during flights over the St. Lawrence River between Québec City and Montréal, we have observed striking differences in the colour and turbidity of the water between one bank and the other, indicative of large cross-flow variations in the seston. Our sampling results from the north and south channels at the downstream end of Île d'Orléans provide evidence that the phytoplankton variability across the northwest–southeast axis of the TZ can be potentially large. For preparation of our samples, we tried to minimize the effects of prefiltration, but the traditional uncertainties remain about the magnitude of filter blockage and leakage effects (e.g., Stockner et al. 1990). We adopted the preservation method of Hall (1991), but did not evaluate the effects of liquid storage on picoplankton cell counts. Our counts would not have included the small-celled prochlorophytes that are known to be important in some aquatic environments (Chisholm et al. 1988) but that can only be detected by flow cytometry or high-pressure liquid chromatography. Each of these aspects will require much closer attention in future studies of the St. Lawrence River. Despite these uncertainties, however, the present study provides clear evidence that photosynthetic picoplankton are an important component of the river–estuary system and that they are subject to large variations in biomass and pigment structure over time and space.

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Summer Diet of the Harbour Porpoise (*Phocoena phocoena*) in the Estuary and the Northern Gulf of St. Lawrence

Pierre-Michel Fontaïne

Département de Biologie, Université Laval, Ste. Foy, QC G1K 7P4, Canada

Mike O. Hammill

Ministère des Pêches et des Océans, Institut Maurice Lamontagne, Mont Joli, QC G5H 3Z4, Canada

Cyrille Barrette

Département de Biologie, Université Laval, St. Foy, QC G1K 7P4, Canada

and Michael C. Kingsley

Ministère des Pêches et des Océans, Institut Maurice Lamontagne, Mont Joli, QC G5H 3Z4, Canada

Fontaine, P.M., M.O. Hammill, C. Barrette, and M.C. Kingsley. 1994. Summer diet of the harbour porpoise (*Phocoena phocoena*) in the estuary and the northern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. 51: 172–178.

Stomach contents (n = 138) were examined in harbour porpoise (*Phocoena phocoena*) caught incidently by commercial fishermen in the estuary and the Gulf of St. Lawrence; 111 stomachs contained food. A total of 4423 otoliths and 11 upper beaks were collected belonging to nine species of fishes and one species of squid. Capelin (*Mallotus villosus*), Atlantic herring (*Clupea harengus*), and redfish (*Sebastes marinus*) were the three most important species in the diet by frequency of occurrence (83, 8, and 4.5%, respectively) and percent occurrence in the stomachs (52, 49, and 8.5%). Capelin and herring also made the greatest mass and caloric contribution to the diet of porpoise (>80%). The estimated mean mass and caloric value of the stomach contents of a nonlactating adults were 958 g and 7007 kJ, respectively.

Cent trente-huit estomacs de marsouins communs (*Phocoena phocoena*) furent retirés de carcasses obtenues grâce à des pêcheurs commerciaux de l'Estuaire et du Golfe du St-Laurent. Parmi ceux-ci, 111 contenaient de la nourriture. Un total de 4 423 otolithes et 11 becs ont été récoltés appartenant à neuf espèces de poissons et une espèce de calmar. Le capelan (*Mallotus villosus*), le hareng de l'Atlantique (*Clupea harengus*) et le sébaste (*Sebastes marinus*) étaient les trois plus importantes espèces du régime alimentaire en terme de fréquence de présence globale (83, 8 et 4,5 % respectivement) et de pourcentage de présence dans les estomacs (52, 49 et 8,5 %). Encore une fois, les capelans et les harengs ont constitué (> 80 %) la plus haute contribution nutritionnelle en terme de masse et de valeur calorique. L'estimation moyenne de la masse et de la valeur calorique d'un contenu stomacal pour un adulte mâle ou femelle non-lactante est de 958 g et 7 007 kJ.

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The harbour porpoise (*Phocoena phocoena*) is a small cetacean found along northern temperate coasts (Gaskin et al. 1974; Gaskin 1984). Throughout their range, they are subject to incidental capture by commercial fisheries (Lear and Christensen 1975; Prescott and Fiorelli 1980; Hanan et al. 1987; Clausen and Andersen 1988). In Canada, recent work has documented a large by-catch in the northern Gulf of St. Lawrence, off the east coast of Newfoundland, and in the Bay of Fundy (Gaskin 1984; Lien 1987; Read and Gaskin 1988; Fontaine et al. 1994). The impact of these catches on the population is poorly known, due to insufficient information on stock discreteness and size in these areas. Gaskin (1984) has suggested that the harbour porpoise in eastern Canadian waters forms three populations and in more recent work suggested that the Bay of Fundy population is threatened by the large incidental catch (Gaskin 1992).

In the Gulf of St. Lawrence, Newfoundland, and Bay of Fundy, the majority of harbour porpoise are captured in gill nets set for Atlantic cod (*Gadus morhua*) and Atlantic herring (*Clupea harengus*) (Lien 1987; Read and Gaskin 1988; Fontaine et al. 1994). In the Bay of Fundy, the only area in Canada where harbour porpoise have been studied intensively, hake (Merlucidae) and herring are important components of their diet. However, very little is known about their diet in other areas of eastern Canada.

An understanding of a species' food habits is not only of biological interest but is also required in order to be able to assess potential or perceived conflicts between marine mammals and commercial fisheries (Murie 1987). In this paper, we examine the food of harbour porpoise caught incidentally by commercial fishermen in the northern Gulf of St. Lawrence and the St. Lawrence River estuary.

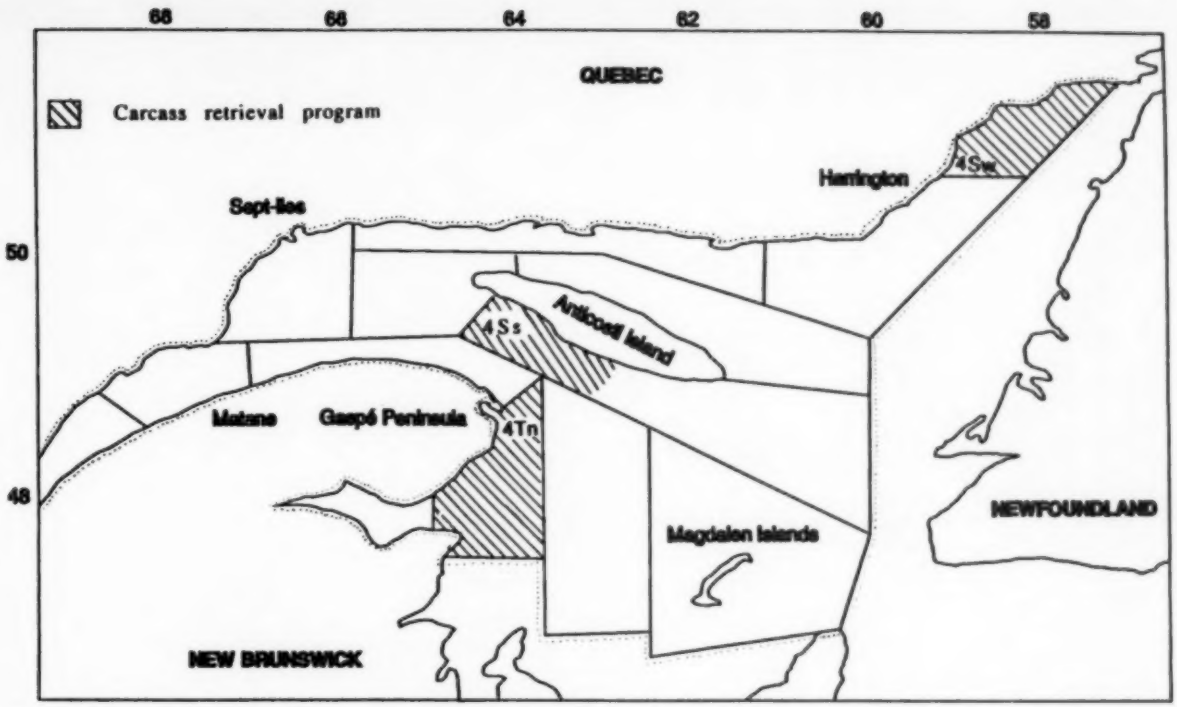

FIG. 1. Study area (enclosed by dotted line). Hatched areas are regions of high catches reported by the carcass retrieval program. Northwest Atlantic Fisheries Organization (NAFO) divisions 4Sw, 4Ss, and 4Tn are shown.

Material and Methods

During May–August 1989, 138 harbour porpoise were obtained from commercial fishermen in the estuary and the Gulf of the St. Lawrence (Fig. 1). Carcasses were obtained mostly from the Lower North Shore (August, $n = 21$), southern Anticosti Island (June, $n = 25$; July, $n = 15$; August, $n = 3$), and the Baie des Chaleurs (May, $n = 2$; June, $n = 3$; July, $n = 15$; August, $n = 27$). Carcasses were frozen as soon as possible and stored at −40°C until dissection. We do not know the exact time between death and freezing. After a standard necropsy (American Society of Mammalogists 1961), the stomach was extracted and frozen until further examination.

The stomach of the harbour porpoise is divided into three compartments (Smith 1972). We examined only the forestomach because the contents of the two remaining compartments are often too digested for otolith measurement and identification (Recchia and Read 1989). The weight of the stomach contents was determined by weighing the forestomach full and empty. Otoliths and partly digested fish were retrieved manually after filtration using two nested sieves with a mesh size of 1.4 and 0.425 mm. Sagittal otoliths and cephalopod beaks were retrieved and stored dry. The remaining contents were stored in 70% ethanol.

Sagittal otoliths were identified to species or to family using a reference collection (Department of Fisheries and Oceans, Institut Maurice-Lamontagne, Mont-Joli, Que.) or a published guide (Härkönen 1986). The cephalopod species were identified using Clark (1986). For each fish species, otoliths were separated into three classes: (1) otoliths extracted from the head, (2) otoliths found free in the forestomach and judged undamaged, and (3) all other otoliths. Otoliths in class 1 or 2 were examined under a binocular microscope at 6–16× and measured with a graduated ocular to the nearest millimetre.

The number of individuals of each species was estimated by dividing the number of sagital otoliths by 2. For cephalopods, we recorded the maximum number of either lower or upper beaks found in the forestomach. The relative importance of food items was evaluated using methods described by Hyslop (1980): (1) the frequency of occurrence of stomachs containing remnants of each prey species, (2) the proportion of each prey species in the total number of prey items, (3) the contribution by mass (percent) of each species of fish, computed from otolith – fish length and fish length – fish weight regressions (Table 1), and (4) the caloric contribution (percent) of the prey species, estimated from the mass of each species ingested and published caloric values for each prey species (Montevecchi and Piatt 1984; Steimle and Terranova 1985; Murie and Lavigne 1991).

Porpoise were assigned to one of four age–sex classes: (1) immature males and females, (2) mature females, with corpus luteum or corpus albicans in the ovaries, as revealed by examining 2-mm-thick slices (Read 1989), (3) lactating females, i.e., with recent ovarian scars and the presence of milk in the mammary glands, and (4) mature males, ≥4 yr of age (Gaskin et al. 1984). Age was determined from tooth sections by reading dentinal and cemental growth layer groups after decalcification and staining in hematoxylin (Matson's, Box 308, Milltown, MT 59851, USA).

TABLE 1. Regression equations used to estimate the mean weights of the prey species. OL = otolith length (mm), Fl = fish length (mm), Fw = fish weight (g).

Prey species	Regression equation	r^2	Source
Mallotus villosus	Fw = 1.163 OL exp 2.742	0.85	Härkönen 1986
Clupea harengus	Fl = 69.23 OL − 27.48	0.96	Recchia and Read 1989
	log Fw = 3.12 log Fl − 5.41	0.99	
Sebastes marinus	Fw = 0.0741 OL exp 3.295	0.99	Härkönen 1986
Scomber scombrus	Fl = 7.33 OL + 0.37	0.90	Recchia and Read 1989
	log Fw = 3.49 log Fl − 2.75		
Gadus morhua	Fl = 3.25 OL − 3.18	0.94	Recchia and Read 1989
	log Fw = 3.04 log Fl − 2.05		

TABLE 2. Number and frequency of occurrence of otoliths found in the stomachs of 111 harbour porpoise.

Prey species	Number of otoliths found	% of stomachs in which they were found	% of otoliths found[a]
Mallotus villosus	3338	52	83.4
Clupea harengus	318	50	7.9
Sebastes marinus	182	8.5	4.5
Scomber scombrus	24	7.5	<1
Gadus morhua	12	4.7	<0.5
Illex illecebrosus	20	7.5	0.5
Sand lance Ammodytidae sp.	84	6.6	2.2
Pleuronectidae sp.	4	0.9	<0.5
Merlucidae sp.	16	1.9	<0.5
Salmonidae sp.	4	0.9	<0.5

[a]This is equivalent to percentage of prey consumed by number.

The Mann–Whitney and Kruskal–Wallis tests were used to compare groups (Scherrer 1984).

Results

Twenty-five of the 138 stomachs examined were empty or contained only unrecognizable otoliths. Two stomachs contained only milk. A total of 4423 sagital otoliths belonging to nine species of teleost fishes were recovered from the remaining 111 forestomachs. Some otoliths (n = 670) were altered beyond recognition and were excluded from the analysis. We also found 10 lower beaks and 11 upper beaks of squid (*Illex illecebrosus*). Sixty-six percent of the stomachs contained only a single species. Herring (*Clupea harengus*), capelin (*Mallotus villosus*), and redfish (*Sebastes marinus*) were the three most important species in the diet by frequency of occurrence and percent occurrence in the stomachs (Table 2). Atlantic mackerel (*Scomber scombrus*), squid, sand lance (Ammodytidae), and cod were also identified but did not exceed 3.5% of prey consumed all together. Members of the families Ammodytidae, Pleuronectidae, Merlucidae, and the Salmonidae could not be identified to species due to otolith erosion, but these accounted for less than 0.5% of all prey.

We compared otolith length in classes 1 and 2. For both capelin and herring, class 2 otoliths were significantly smaller than class 1 otoliths (capelin, P = 0.001; herring, P = 0.017). Since mackerel also have thin fragile otoliths, we used only class 1 otoliths for these three species to reconstruct mean fish weight. Larger otoliths, from redfish and cod, are eroded more slowly in the stomach (Recchia and Read 1989). Because our sample was small, we used both class 1 and 2 otoliths for the estimation of redfish and cod body weight (Table 3). For squid and sand lance, it was not possible to estimate their mean weights with our material. Squid were assumed to have a mean weight of 58 g (Recchia and Read 1989). We also assumed that porpoise consumed adult sand lance with a mean weight of 11.6 g (Vladykov 1946; Brêthes et al. 1992).

Caloric values were available for only six of the 10 species consumed, but these accounted for 97% of the items eaten (Table 2). Capelin and herring made the greatest mass and caloric contribution to the food intake of porpoises (>80%) (Table 3). Redfish and mackerel were the third and fourth most important species, but combined, these two species represented less than 18% of the mass and caloric contribution. Cod and squid contributed less than 2 and 1%, respectively, of the mass and caloric intake.

The mean length of the principal prey species consumed was 28 cm (SD = 9; range 13–40 cm; Fig. 2). Capelin were the smallest prey (13.8 ± 0.8 cm, n = 23) and mackerel the largest (37.7 ± 1.6 cm, n = 10). Prey size was not related to porpoise age or sex.

Analysis of porpoise diet was complicated by the seasonal and regional nature of the carcass collections. Porpoise obtained from the Lower North Shore were captured in August, while 18 of the 30 Anticosti animals were captured in June and 23 of the 36 specimens from the Baie des Chaleurs were captured between the 10 July and 9 August. The sex ratio did not differ significantly from 1:1 in all

TABLE 3. Estimated weights of different prey species and their relative mass and caloric contribution to the harbour porpoise diet.

Prey species	Mean prey weight (g ± SD)	Caloric values (kJ/g)	Mass contribution (%)	Caloric contribution (%)
Mallotus villosus	23.0 ± 3.7 (n = 23)	10.4[a]	37.6	40.2
Clupea harengus	277.7 ± 53.8 (n = 47)	10.6[b]	43.0	48.5
Sebastes marinus	116.2 ± 55.7 (n = 7)	5.14[c]	10.3	5.9
Scomber scombrus	573.4 ± 83.1 (n = 10)	6.0[b]	7.0	4.3
Gadus morhua	256.9 ± 47.6 (n = 5)	4.2[b]	1.4	0.6
Illex illecebrosus	58[d]	7.1[b]	0.6	0.4
Sand lance (Ammodytidae)	11.6[e]		0.5	

[a]Montevecchi and Piatt (1984).
[b]Steimle and Terranova (1985).
[c]Murie and Lavigne (1991).
[d]From Recchia and Read (1989).
[e]From Vladykiv (1946).

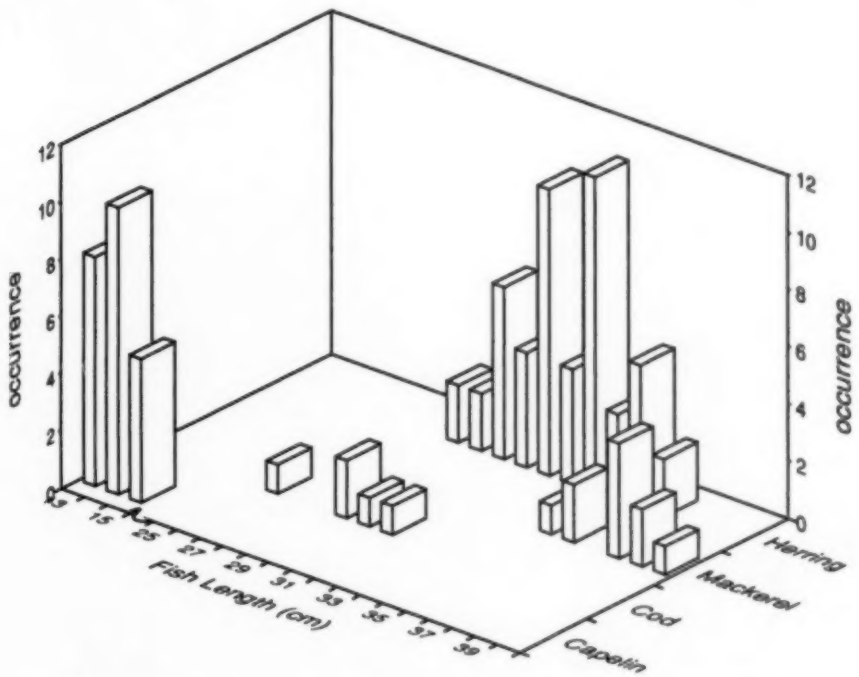

FIG. 2. Frequency distribution of the length of some prey species found in the harbour porpoise stomachs examined.

areas. The proportion of mature animals in the catch increased from the Baie des Chaleurs to the Lower North Shore (Table 4).

Differences in diet composition of harbour porpoise were observed among regions. Sixty-one percent of the mass contribution of the porpoises' diet from the Baie des Chaleurs was represented by herring and only 18% by capelin. Along the south coast of Anticosti Island, porpoise fed more on capelin (59%) than herring (11%), and from the Lower North Shore they fed almost entirely (90%) on capelin (Table 4). Mature porpoise consumed more capelin (P = 0.007) and redfish (P = 0.016) than immature specimens, while the latter preferred herring (P = 0.07) and sand lance (P = 0.042). However, these differences are clearly influenced by the geographic distribution of the samples (i.e., preponderance of immature animals from the Baie des Chaleurs, who had consumed mostly herring).

There were no significant differences among age–sex classes in terms of prey mass consumed even after correcting for the larger body size of females (kilograms$^{0.7}$, Kleiber 1975) (Table 5).

Discussion

Fish otoliths or cephalopod beaks are often used to identify the prey species in the diet of piscivorus marine mammals and to estimate their relative importance (Fitch and Brownell 1968; Murie and Lavigne 1991). These dense and

TABLE 4. Mass contribution of the two main fish species found in harbour porpoise stomachs for different NAFO divisions with the proportion of mature harbour porpoise in each group.

NAFO division	Sample size	Sex ratio (M:F)	Proportion of mature (%)	Mass (%) of:	
				Capelin	Herring
4Sw	15	7:8	75	90	0
4Ss	30	14:16	63	59	11
4Tn	36	18:18	36	13	61

TABLE 5. Absolute (G ± SD) and relative ($g/kg^{0.75}$ metabolic body weight ± SD) prey mass consumed, caloric intake (kJ and $kJ/kg^{0.75}$), and forestomach content mass (g) for five age–sex classes of porpoise.

Age–sex class	*n*	Prey mass consumed		Caloric intake		Absolute forestomach content
		Absolute	Relative	Absolute	Relative	
Immature males	30	601 ± 532	38 ± 34	5332 ± 5142	159.7 ± 121.8	376 ± 395
Immature females	20	785 ± 768	49 ± 50	6678 ± 7092	184.2 ± 174.6	439 ± 429
Mature males	21	956 ± 977	46 ± 45	5615 ± 5818	208.4 ± 221.6	279 ± 323
Nonlactating females	14	976 ± 1821	58 ± 123	8400 ± 18959	244.1 ± 543.2	417 ± 337
Lactating females	18	1090 ± 773	53 ± 37	6559 ± 5051	193.4 ± 141.9	419 ± 349

hard structures are resistant to digestion (Treacy and Crawford 1981; Clark 1986) and possess diagnostic features making their identification relatively easy (Jobling and Breiby 1986). However, certain biases are associated with this technique. Variability in digestibility and retention of squid beaks and otoliths in the stomach will affect estimates of number of individuals in the diet, frequency of occurrence, and estimates of mass and caloric contributions, calculated from otolith – fish length and fish length – fish weight relationships (Bigg and Fawcett 1985; Da Silva and Neilson 1985; Recchia and Read 1989).

The caloric value of whole fish is affected by body size, reproductive state, and seasonal changes in fat content which vary between stocks (Jobling and Breiby 1986; Hislop et al. 1990). The caloric value of capelin may vary from as low as 3.9 kJ/g to as high as 9.4 kJ/g (Montevecchi and Piatt 1984). To date, few studies have taken into account these seasonal changes in caloric content in diet reconstructions. However, this is not a simple task. In our study area, there are at least three populations of herring. Two populations spawn in the spring, while the third spawns in the fall, and one of the populations spawning in spring is characterized by smaller length-at-age than the other two populations (Coté et al. 1980).

The majority of stomachs (66%) contained only one prey species. Similar results have been reported in grey seals (*Halichoerus grypus*) (Benoit and Bowen 1990) and in harp seals (*Phoca groenlandica*) (Murie and Lavigne 1991), suggesting that many marine mammals typically feed on small schooling species.

Throughout its range, the diet of the harbour porpoise appears to be dominated by commercially important clupeoids and gadoids such as herring, cod, and hake (Wilke and Kenyon 1952; Rae 1965, 1973; Smith and Gaskin 1974; Recchia and Read 1989). In this study, gadoids such as cod and hake were consumed but these formed only a minor component in the overall diet. Instead, we found that capelin and herring were the most important prey items in terms of frequency of occurrence and mass and caloric contribution to the diet. Capelin are also major prey items in the diet of beluga (*Delphinapterus leucas*) (Vladykov 1946), harp seal (Murie and Lavigne 1991), grey seal (Benoit and Bowen 1990), cod (Lilly 1987), and many seabirds (Winters 1975), underlining the importance of this species to the Gulf of St. Lawrence ecosystem. In the Gulf of St. Lawrence, capelin is more abundant along the north shore than along the south shore (Bailey et al. 1977), while for herring the opposite is true (Coté et al. 1980). These distributions correspond with the differences in mass ingested and the frequency of occurrence of these species observed in the stomachs of porpoise at different locations of the incidental catches (Table 4).

Using the mean number of otoliths found in a stomach, the estimated mean mass and caloric value of food ingested by a nonlactating adult porpoise was 958 g and 7007 kJ, which are similar to the values of 722 g and 7486 kJ, respectively, obtained by Recchia and Read (1989) in the Bay of Fundy. Andersen (1965) found that an adult porpoise in captivity required 4.3 kg (22 300 kJ/d) or approximately 10% of its body weight. However, this estimate may be too high due to the opportunistic feeding behaviour of the porpoise which is known to gorge when food is plentiful (Yasui and Gaskin 1986). Other estimates suggest that the daily energy requirement for an adult porpoise would be 11 200–17 260 kJ/d or approximately 3.6 × basal metabolic rate (BMR) (Yasui and Gaskin 1986; Worthy et al. 1987). Using this figure (3.6 × BMR), adult harbour porpoise would require three times the quantity of food recorded in their stomachs to satisfy their daily energy requirement.

In small cetaceans, lactating females are assumed to require more energy than other mature adults (Bernard and Hohn 1989). Recchia and Read (1989) reported that lactating females in the Bay of Fundy had a significantly higher caloric and prey mass intake than other mature classes. However, we did not observe differences between lactating females, juveniles, nonlactating females, and male porpoise. Andersen (1965) found that captive male harbour porpoise ate less than females, but when scaled to body $weight^{0.75}$ the difference vanished.

In eastern Canada, groundfish gill nets are responsible for most of the harbour porpoise by-catch (Lien 1987; Read and Gaskin 1988; Fontaine et al. 1994). In the Bay of Fundy, it is believed that the harbour porpoise population is threatened due to the large incidental catch (Gaskin 1992). There, an indirect relationship between commercial fishing for groundfish and harbour porpoise entrapments has been documented because both commercial groundfish and porpoise actively prey on hake and herring (Read and Gaskin 1988; Recchia and Read 1989). A large incidental catch of porpoise has also been documented in the northern Gulf of St. Lawrence, but its impact on the population is not known due to insufficient information on population size. As in the Bay of Fundy, an indirect relationship is also observed in the Gulf of St. Lawrence. Although 95% of entrapped porpoise are caught in cod gill nets (Fontaine et al. 1994) cod are present in only a small fraction of the stomachs examined (4.5%). In the Gulf, cod, harbour porpoise, and other marine mammals feed on capelin or small herring (Vladykov 1946; Lilly 1987; Scott and Scott 1988; Benoit and Bowen 1990; Murie and Lavigne 1991). Thus, it would appear that harbour porpoise become entangled in groundfish nets set for cod while foraging for capelin and herring.

The size frequency of fish consumed by the harbour porpoise is important in assessing the impact of porpoise on commercial fisheries. Most cod harvested commercially are >40 cm long (Fréchet 1987), while porpoise consume only cod <32 cm in length, prerecruits to the commercial fishery. Normally some of these prerecruit fish would die from other sources of mortality, before reaching a size to be harvested by the commercial fishery (Murie and Lavigne 1991). However, the relationship between natural mortality in prerecruit fish, losses of large numbers of small fish to top predators such as whales or seals, and the future effects of these losses to the commercial fishery need to be examined in more detail.

Capelin enter into the commercial fishery at a mean length of about 13 cm (J-D. Lambert, Department of Fisheries and Oceans, Mont-Joli, Que., personal communication). In our reconstructed lengths of capelin in harbour porpoise stomachs, all individuals consumed were >13 cm, large enough to be taken commercially. Herring are harvested at lengths of >28 cm (Trudeau and McQuinn 1986). In our reconstructed diets, 96% of the herring consumed by porpoise were sufficiently large to be taken by commercial fisheries. Similar results were obtained for mackerel. This species is harvested by the commercial fishery at a length of >35 cm, which also overlaps the size range consumed by porpoise (F. Grégoire, Department of Fisheries and Oceans, Mont-Joli, Que., personal communication).

However, our results must be interpreted with caution. The samples were obtained from a by-catch associated with commercial fishing activity. Without information on the distribution of the porpoise population in the northern Gulf of St. Lawrence, it is difficult to determine how representative our samples are. Although our results would suggest that porpoise may have an effect on commercial fisheries, the high incidental catch of porpoise reported in the Gulf (Fontaine et al. 1994) suggests that commercial fishing activity may also have a negative impact on porpoises. Currently there is insufficient information available to address either of these concerns.

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Turbidity and Temperature Effects on Oxygen Consumption in the Zebra Mussel (*Dreissena polymorpha*)

James E. Alexander, Jr., James H. Thorp, and Ronald D. Fell

Department of Biology, University of Louisville, Louisville, KY 40292, USA

Alexander, J.E. Jr., J.H. Thorp, and R.D. Fell. 1994. Turbidity and temperature effects on oxygen consumption in the zebra mussel (*Dreissena polymorpha*). Can. J. Fish. Aquat. Sci. 51: 179-184.

The effects of acute exposure to suspended inorganic sediment (bentonite clay) on oxygen consumption rates of the zebra mussel (*Dreissena polymorpha*) were examined to estimate their maintenance costs for colonizing the Ohio River. Adult *D. polymorpha* were acclimated to 10, 18, or 26°C for 2 wk (10 replicate groups for each acclimation temperature) and respiration was measured in a closed recirculating system using oxygen electrode probes. Each replicate group of mussels was tested at their acclimation temperature under five turbidity levels: 0 (clear water), 5, 20, 80, and 160 NTU (nephelometric turbidity units). Respiration rates were significantly affected by acclimation temperature (direct relationship) and turbidity (inverse relationship, which leveled off with increasing turbidity). Warmer-acclimated animals showed a more dramatic drop in oxygen consumption with increasing turbidity, and all size-classes were equally affected by turbidity. Our results suggest that the normal ranges of temperatures and turbidity levels in the Ohio River may depress growth rates of adult *D. polymorpha* by increasing maintenance costs but probably will not by themselves prevent establishment of viable populations in this river.

Nous avons examiné les effets d'une exposition aiguë à des sédiments inorganiques en suspension (bentonite) sur la consommation d'oxygène de la moule zébrée (*Dreissena polymorpha*) afin d'estimer quelle serait la dépense d'entretien d'une population qui coloniserait le fleuve Ohio. Des adultes de *D. polymorpha* ont été acclimatés à 10, 18 ou 26°C pendant 2 sem (10 groupes parallèles pour chaque température d'acclimatement), et nous avons mesuré leur respiration dans un système clos à recirculation en utilisant des électrodes indicatrices d'oxygène. Chaque groupe de moules a fait l'objet d'un test à sa température d'acclimatement à cinq niveaux de turbidité : 0 (eau claire), 5, 20, 80 et 160 NTU (unités de turbidité néphélémétrique). Les taux de respiration étaient nettement affectés par la température d'acclimatement (relation directe) et par la turbidité (relation inverse, qui plafonnait quand la turbidité s'accroissait). Les animaux acclimatés à une température plus élevée présentaient une chute plus spectaculaire de la consommation d'oxygène avec la hausse de la turbidité, et toutes les classes de taille étaient également affectées par la turbidité. Nos résultats semblent indiquer que les fourchettes normales de température et de turbidité dans le fleuve Ohio peuvent affaiblir le taux de croissance des *D. polymorpha* adultes en accroissant leur dépense d'entretien, mais ne peuvent probablement pas en elles-mêmes empêcher l'établissement de populations viables de l'espèce dans le fleuve.

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Since its colonization of the Great Lakes in the mid-1980s (Hebert et al. 1989), the zebra mussel (*Dreissena polymorpha*) has spread rapidly to the major river systems in southeastern Canada and the central and eastern portions of the United States, such as the St. Lawrence, Hudson, Mississippi, and Ohio rivers. The potential area for zebra mussel colonization, based on current estimates of the effect of temperature and water hardness on adult survival and reproduction, includes much of the northern two thirds of the United States and the southern part of Canada (Strayer 1991).

Because of the tremendous economic impact of *D. polymorpha* (e.g., from biofouling of raw-water intake systems, Mackie et al. 1989) and their potentially severe ecological effects on native unionid mussels and other benthic and pelagic species (Hebert et al. 1991; Mackie 1991; Hunter and Bailey 1992; MacIsaac et al. 1992; Griffiths 1993), North American research on zebra mussels (*Dreissena* spp.) is currently in a boom phase. A second, currently unnamed species, the quagga mussel (*Dreissena* sp., May and Marsden 1992), has also colonized the Great Lakes; the quagga mussel may differ from the zebra mussel *D. polymorpha* in its ecological and physiological tolerances. In addition to their detrimental influence on unionids and other species, many aspects of *Dreissena*'s biology are being, or have been, examined; these include their impacts on turbidity, food levels, and water quality (Mackie et al. 1989; Hebert et al. 1991; MacIsaac et al. 1992), as well as the effects of temperature on zebra mussel growth, reproduction, filter-feeding, and respiratory activities (Morton 1969, 1971; Garton and Haag 1991; J.E. Alexander, Jr. and R.F. McMahon, unpublished data).

To date, almost all published papers on the spread of *D. polymorpha* and their ecological impacts in North America and Europe have been on lake populations, despite the fact that *D. polymorpha* is found in lentic and lotic habitats of both continents. Consequently, very little information exists for predicting the potential success of *D. polymorpha* in floodplain rivers (Strayer 1991).

As zebra mussels have dispersed southward from the Great Lakes into inland rivers, they have encountered higher temperatures and inorganic suspended loads (turbidity). While the biological effects of temperature, nutrients, and light on many organisms are well established, much less is known concerning the impact of turbidity on colonization rates, population growth, or bioenergetics in general (see Wilber 1983 for a review of turbidity effects in aquatic systems). Therefore, our main objective was to evaluate the effect of temperature and acute exposure to turbidity on the oxygen consumption of *D. polymorpha*. Our ultimate goal was to predict the success of these bivalves in the Ohio River and other large rivers of North America.

Materials and Methods

Collection and Maintenance

Dreissena polymorpha obtained from Lake Erie (Ohio River populations were currently too sparse for experimental use) were acclimated to three different temperatures, 10, 18, and 26°C (±1°C) for at least 14 d in environmental chambers. We only selected the zebra mussel *D. polymorpha*; no quagga mussels (*Dreissena* sp.) were used in these experiments. During this period, the mussels were maintained in plastic tubs (0.1 m^2 × 17.5 cm deep) containing 5 L of aerated, reconstituted standard freshwater ("hard" water type, APHA 1985). The mussels were fed approximately 100 mL of a mixed-algae stock solution two or three times weekly during the acclimation period, but feedings were discontinued 3 d prior to and during the experiment.

Three days before each experiment, we selected a total of 10 replicate groups of *D. polymorpha* for each acclimation temperature treatment (10, 18, and 26°C). All individuals in a replicate group were of similar size (±1 mm); the numbers of animals in each replicate group (ranging from 3 to 20 individuals) depended on acclimation temperature and body size. We used two replicate groups from each of five size-classes: 14, 16, 18, 20, and 22 mm maximum shell length. During the 3-d pretest interval and throughout the week-long test period, the replicate groups were kept at their acclimation temperature, and each group was housed separately in small plastic containers (81 cm^2 × 13 cm deep) containing 400 mL of reconstituted standard freshwater which was changed periodically. Several variables affect oxygen consumption in bivalves, such as animal size and group size (Patterson 1983; McMahon 1991), although zebra mussels may differ from other bivalves in their response to group size because they exist in very high densities in the field. However, oxygen consumption rates were obtained for every replicate group at all turbidities, eliminating the potential confounding effect of group size; the same size-classes were used in each acclimation temperature group to minimize the confounding effect of animal size.

Oxygen Update Measurement

Oxygen consumption rates for each group of zebra mussels were determined daily at their acclimation temperatures (±1°C) in both clear water and one of four turbidity levels, with rates calculated for all four turbidity conditions over the course of a week. Oxygen consumption was measured directly with a Clark-type polarographic oxygen electrode (YSI biological oxygen monitor, model 5300), coupled with a chart recorder, using a method described elsewhere (McMahon 1985). Respiration rates were expressed as microlitres of oxygen consumed per milligram of dry tissue weight per hour at STP, or $\dot{V}O_2$.We measured oxygen consumption for mussels randomly exposed to five concentrations of suspended inorganic particles (bentonite clay): 0, 5, 20, 80, and 160 NTU (nephelometric turbidity units, Wilber 1983). Approximately 1 g of bentonite clay is equal to 160 NTU (value calculated from a regression of data obtained with a Hach turbidimeter, model 2100A).

An experimental run consisted of four sequential steps: (1) a 5-min habituation period with the mussels in clear water (0 NTU), (2) a 20-min measurement period with mussels in clear water, (3) a second 5-min habituation interval during which time the animals were first exposed to one of four turbidity levels (5–160 NTU), and (4) a final 20-min measurement period at the turbid condition. In most cases, the habituation period was sufficiently long to allow time for mussels to open their valves, extend their siphons, and begin filtering. During habituation and measurement periods, mussels occupied the respiratory chamber, which consisted of a clear glass cylinder 9 cm long and 2.6 cm outer diameter (rubber stoppers were present at each end). All water had been cooled or heated to the acclimation temperature and aerated to ensure full oxygen saturation (partial pressure of oxygen, $P_{O_2} \approx 20.53$–20.93 kPa). A perfusion pump (Gilson Minipuls perfusion pump, model 312) circulated water in a complete circuit through perfusion tubes (0.5 cm outer diameter) into and out of the respiratory chamber and past the oxygen electrode at 20 mL·min^{-1}. A Cole-Palmer perfusion pump (model 7520-00) was used to pump fluids from the water bath through the microelectrode chamber to maintain it at the acclimation temperature. During the 20-min measurement periods, P_{O_2} in the chamber generally dropped in a linear fashion by approximately 5–25% as the mussels respired oxygen. For each replicate group, whole-animal oxygen consumption rates ($\dot{V}O_2$, microlitres of oxygen consumed per hour at STP) were calculated using linear regression analyses on the drop in P_{O_2} over the 20-min measurement period (McMahon 1985).

Dry biomass values were employed to calculate weight-specific oxygen consumption rates ($\dot{V}O_2$); shell-free, tissue dry weights were determined by the procedures of McMahon (1985). After each group of animals had been tested at all four turbidities, they were frozen for several weeks before being submerged in a 10% nitric acid solution. This solution digested much of the shell; after a few minutes the respirable tissue mass was separated from the shell remains and byssus. After rinsing this tissue in clean water, it was placed in a drying oven at 85°C for several days until a constant weight was achieved.

Statistical Analysis

Data were analyzed with parametric procedures (repeated measures ANOVA and Tukey's HSD test) of the Statistical Analysis System (SAS Institute Inc. 1990) after a normality test showed no significant departure of the data from a normal distribution. An alpha level of ≤0.05 was used to indicate significance of tests. Statistical procedures to examine specific hypotheses are described in appropriate sections of the Results and Discussion.

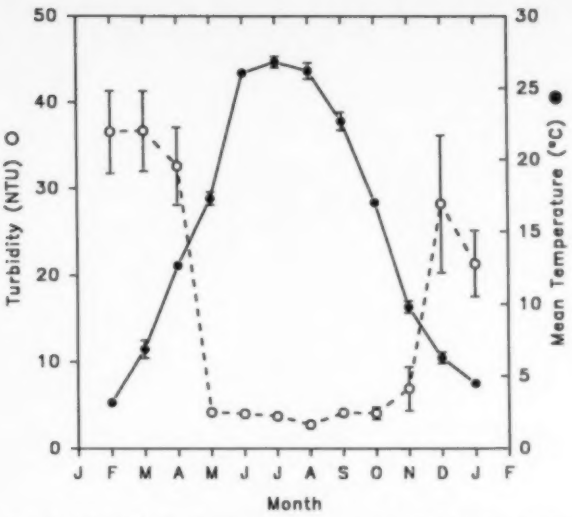

FIG. 1. Monthly mean temperatures and turbidity levels of nine sites in the three navigation pools of the Ohio River nearest Louisville, Kentucky, from February 1991 to January 1992. The error bars are standard errors of the means.

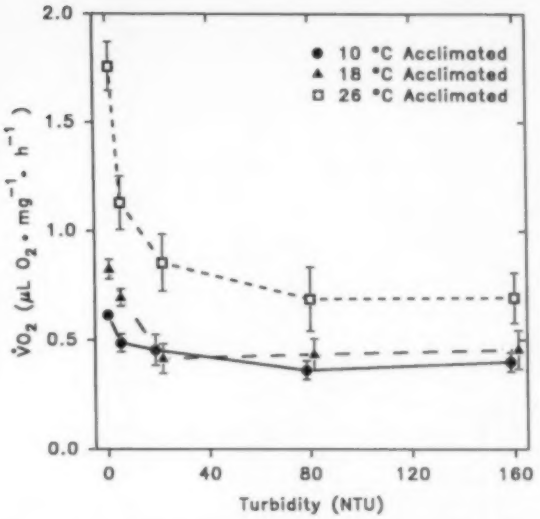

FIG. 2. Respiratory response ($\dot{V}O_2$) of zebra mussels to acute exposure to various levels of turbidity. Zebra mussels were acclimated to three different temperatures and were tested at their acclimation temperature. The error bars are standard errors of the means. Some data points were slightly offset horizontally for clarity.

Seasonal Patterns of Temperature and Turbidity in the Ohio River

We chose these experimental temperatures and turbidities based on recent seasonal patterns of these two important abiotic variables along a 450-km stretch of the Ohio River near Louisville, Kentucky (Fig. 1). The open-channel values were very similar to those obtained in deep water and near the shoreline, typical of well-mixed rivers. As is evident in Fig. 1, turbidity and temperature vary inversely with each other; this primarily noncausal relationship results from other factors, such as the seasonal pattern of river discharge. Turbidity levels are usually highest (typically 20–40 NTU) during the winter and early spring when temperatures are low (about 3–10°C). Temperatures gradually rise to a summer peak of approximately 26°C, and turbidity drops to about 4–5 NTU as a result of decreased flow. The mean daily suspended sediment in the Ohio River ranges from 8 to 510 mg·L^{-1} (Pearson 1992); the latter suspended sediment value corresponds to a bentonite turbidity reading of approximately 80 NTU.

Results and Discussion

Temperature and Turbidity Effects on Respiration

Animals acclimated at warmer temperatures had significantly higher $\dot{V}O_2$ rates than mussels acclimated at lower temperatures (Fig. 2; Table 1), as is commonly seen for ectothermic animals. The increase in oxygen consumption with a 10°C increase in acclimation temperature (acclimation Q_{10} or $Q_{10(Acc.)}$, McMahon 1991) was 1.96 over the temperature range of 10–26°C in clear water. The metabolic rates observed in clear water agree closely with data from J.E. Alexander, Jr. and R.F. McMahon (unpublished data), Garton and Haag (1991), and Quigley et al. (1993). In general, oxygen consumption of freshwater bivalves varies tremendously from season to season; oxygen consumption in summer months may be 230–3300% of that during the winter months, depending on species, body size, and temperature range (reviewed in McMahon 1991). Our data suggest that *D. polymorpha*'s seasonal response to temperature is intermediate compared with all bivalves; $\dot{V}O_2$ at 26°C was 320% higher than $\dot{V}O_2$ observed at 10°C in clear water.

Overall oxygen consumption rates declined significantly with increasing turbidity at all three acclimation temperatures (Table 1), but the relationship between oxygen consumption and turbidity was not linear (Fig. 2). Oxygen consumption neither ceased nor continued to decline at very high turbidity levels: $\dot{V}O_2$ leveled off at 40–70% of the rates observed in clear water (Fig. 2). Significant interactions between turbidity and temperature were present (Table 1); oxygen consumption levels dropped more rapidly with increasing turbidity for warmer-acclimated mussels than for cooler-acclimated mussels. No interactions were present between turbidity and respiration of replicate size groups at a given temperature (Table 1), suggesting that smaller and larger animals were equally affected by turbidity.

Because each replicate had a clear-water and a turbid-water $\dot{V}O_2$ measurement on each day, a paired *t*-test (two-tailed) could be conducted on each day's results. For each combination of acclimation temperature and turbidity, all paired *t*-test values were significant ($p < 0.01$, with the exception of the comparison of 0–5 NTU in 10°C animals, which was nearly significant at $p < 0.1$), indicating that an acute exposure to small amounts of suspended solids depressed respiration in *D. polymorpha*.

To test for significant differences in mean oxygen consumption among turbidity levels, we used Tukey's HSD test on each temperature treatment (Table 2). In general, oxygen consumption in clear water (0 NTU) was significantly

TABLE 1. Repeated measures ANOVA examining the impact of temperature and turbidity on respiration in the zebra mussel.

Source of variation	df	MS	F	P
Model	149	0.51	8.10	0.0001
Error	90	0.06		
$r^2 = 0.93$, CV = 30.46				
Temperature[a]	2	5.32	16.00	0.0001
Turbidity[b]	4	3.69	49.53	0.0001
Temperature × turbidity[b]	8	0.83	11.15	0.0001
Size-class (within temperature)	27	0.33	5.26	0.0001
Turbidity × size-class (within temperature)	108	0.07	1.18	0.2104

[a]Error term = size-class (within temperature).
[b]Error term = turbidity × size-class (within temperature).

higher than that recorded at all turbidities (Table 2); this was especially evident at the 10 and 26°C acclimation runs.

Because the same animals were repeatedly tested throughout a week, their respiratory responses could have changed over time if they were progressively stressed by the experiment. To determine whether this systematic error occurred, we ran a repeated measures ANOVA on the clear-water $\dot{V}O_2$ values obtained each day for each replicate group. An univariate test of hypotheses for within-subject effects revealed no significant effects of time on oxygen consumption (ANOVA, $F_{3,81} = 0.14$, $p < 0.94$), suggesting that *D. polymorpha* were not progressively stressed during the week-long experimental trials.

TABLE 2. Tukey's range (HSD) test for significant differences among all mean ($\dot{V}O_2$) values obtained at all five turbidity levels. Results for each acclimation temperature were analyzed separately. For any given temperature, different letters indicate that oxygen consumption rates recorded for two or more turbidity levels were significantly different ($p < 0.05$).

Temperature (°C)	Turbidity (NTU)				
	0	5	20	80	160
10	a	ab	b	b	b
18	a	ad	bc	bc	bd
26	a	b	b	b	b

Metabolic Temperature Acclimation

Like many ectothermic species, some bivalves have the ability (at least partially) to adjust their metabolic rates in response to seasonal fluctuations in temperature. This seasonal metabolic temperature acclimation allows the maintenance of an optimal metabolic rate throughout the year; it can be detected by examining the $Q_{10(Acc.)}$ values (reviewed in McMahon 1991). A $Q_{10(Acc.)}$ value near 1.0 suggests that metabolic acclimation is perfect for that species, with $\dot{V}O_2$ held constant throughout the year (metabolic rates adjust upwards after acclimation to warmer temperatures). Species with $Q_{10(Acc.)}$ values near 2.0 have no metabolic acclimation, and $Q_{10(Acc.)}$ values greater than 3.0 demonstrate inverse metabolic acclimation (McMahon 1991). The $Q_{10(Acc.)}$ of 1.96 (10–26°C) suggests that *D. polymorpha* has little capacity for metabolic temperature acclimation.

Effects of Turbidity on Metabolism

In comparison with the relative abundance of studies on the effect of suspended solids on filter-feeding and growth in bivalves (Foster-Smith 1975; Winter 1978; Widdows et al. 1979; Kiorboe et al. 1981; Foe and Knight 1985; Way et al. 1990) and for *D. polymorpha* in particular (Morton 1971; Sprung and Rose 1988; Reeders and Bij de Vaate 1990; Wisniewski 1990), little information exists on the effects of suspended solids and food concentrations on respiration. Normal levels of inorganic suspended particulate matter have been shown to have moderate to relatively little effect on oxygen consumption in some freshwater and marine bivalves (Widdows et al. 1979; Aldridge et al. 1987). The basic mechanism causing the drop in oxygen consumption with increasing turbidity is unclear, in large part because relatively little research has been conducted on this subject. Higher concentrations of suspended materials can depress growth rates by overloading the gut and gills with inorganic solids (Morton 1971). Suspended solids may interfere with respiration and filter-feeding by fouling water currents passing over the gills (Aldridge et al. 1987; McMahon 1991) or by physically impeding gas exchange across cell membranes of epithelial cells lining respiratory surfaces.

Dreissena polymorpha may be able to adjust their filtration or clearance rates somewhat, which may partially explain the nonlinear relationship between respiration and turbidity evident from our data. Way et al. (1990) demonstrated that the Asiatic clam *Corbicula fluminea* may make physiological adjustments in response to changing environmental conditions (e.g., variable levels of suspended loads), thus maintaining an approximate constancy or optimality of their filtration rates. At higher suspended load concentrations, pseudofeces are formed in many bivalves; this mechanism may help clear the gills for respiratory and filter-feeding purposes. Our data reveal the immediate, acute effect of turbidity on the respiration of zebra mussels, not the chronic effect of long-term exposure to high turbidity levels. Under chronic conditions, the mussels may adapt to the turbid conditions by becoming more efficient in filtering out undigestible inorganic particles from the gills, thus possibly maintaining a metabolic rate higher than that measured in response to acute turbidity stress.

Our results suggest that the normal seasonal changes in temperature and turbidity levels in rivers will significantly influence aerobic respiration rates in *D. polymorpha*; thus, it could be predicted that growth and reproduction may also be affected. Seasonal differences in oxygen uptake to nitrogen excretion ratios (O:N ratios) demonstrate changes in

the physiological state of the animals as they shift between carbohydrate-based catabolism (high O:N ratios) and protein-based catabolism (low O:N ratios) in response to seasonal changes in temperature (Quigley et al. 1993) and turbidity (Aldridge et al. 1987).

Implications for River Colonization

Dreissena probably entered the Great Lakes as early as 1985 or 1986 (Hebert et al. 1989) but were not discovered in the Mississippi River drainage until 1991. It is not surprising, therefore, that the vast amount of recently published literature on this species concerns lentic populations. While lake studies are useful for understanding some aspects of the biology of lotic populations, the environmental conditions of lakes and rivers are sufficiently different to make predictions on the success of *Dreissena* in rivers uncertain. Two potentially major abiotic differences are the greater thermal mixing and higher inorganic sediment load of rivers. As is evident from our data, temperature and turbidity have a significant interactive effect on respiration in adult *D. polymorpha*. Oxygen consumption declines in a nonlinear fashion with increasing inorganic turbidity, and the effect is significantly more pronounced at higher temperatures.

Our data (Fig. 2) indicate that the most stressful condition for adult *D. polymorpha* would be when both temperature and turbidity are high; however, for the Ohio River, turbidity tends to vary inversely with temperature through time (Fig. 1). Oxygen consumption during the summer will tend to peak because temperatures are high and inorganic sediment load is generally low. In contrast, during the winter, oxygen consumption generally reaches its ebb because of low water temperatures and high inorganic turbidities. However, the impact of increasing turbidity on zebra mussel respiration is greatest in warmer months. Therefore, the effect of heavy precipitation in the river's drainage basin (producing high discharges and turbidities) will be more noticeable in the summer. If oxygen consumption levels diminish with increasing turbidity, and basic energy demands remain constant, *D. polymorpha* may depend more on anaerobic respiration to help satisfy energy demands during some times of the year. Because aerobic respiration is more energetically efficient, the amount of energy available for growth and reproduction would drop unless the supply of assimilated energy rises.

The discoveries of adults and veligers in many rivers of central and eastern North America demonstrate that *D. polymorpha* can survive in our rivers, but this information is inadequate by itself to predict the ultimate success of these exotic molluscs. Our data demonstrate that inorganic sediment load has a detrimental impact on mussel metabolism, especially at high temperatures. Although high turbidities and temperature generally occur at different times in the Ohio River, the relative impact of increasing turbidities on metabolic functions will probably be most dramatic during the short but often severe summer storms. We predict that the zebra mussels in large floodplain rivers will not attain the high densities characteristic of less turbid, lentic ecosystems. However, our results are based on acute responses of adults to turbidity; thus, the chronic effects of turbidity, the possible adaptations to chronic turbidity, and the effects of turbidity on veligers still need to be examined.

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Manganese Reduction in Oneida Lake, New York: Estimates of Spatial and Temporal Manganese Flux

Carmen Aguilar[1] and Kenneth H. Nealson

University of Wisconsin-Milwaukee, Center for Great Lakes Studies, 600 E. Greenfield Ave., Milwaukee, WI 53204, USA

Aguilar, C., and K.H. Nealson. 1994. Manganese reduction in Oneida Lake, New York: estimates of spatial and temporal manganese flux. Can. J. Fish. Aquat. Sci. 51: 185–196.

Manganese is a very reactive redox metal, which exhibits a strong annual cycle in Oneida Lake, New York. Different methods were used to measure Mn(II) fluxes from the sediments throughout the year: (1) estimates based on changes in porewater profiles, (2) direct measurements with in situ flux chambers, (3) concentration gradients into the sediment–water interface in laboratory-incubated cores, and (4) changes in hypolimnetic manganese inventories during stratification. In deep basins of the lake, high rates of Mn(IV) reduction, up to 2.1 $mmol \cdot m^{-2} \cdot d^{-1}$, were observed during the summer and early fall, with little reduction taking place during the rest of the year. In the shallow areas of the lake, where ferromanganese nodules and crusts are commonly found, there was little or no reduction throughout the year. The manganese cycle is tightly coupled to the carbon cycle, based on our findings, and has a significant role in the oxidation of organic carbon in the lake, derived from the high photosynthetic production and the biomass that collapses and reaches the sediment–water interface. Preliminary experiments with poisoned controls suggest that Mn(IV) reduction is the result of a combination of biological and abiological processes.

Le manganèse, métal très réactif dans les réactions d'oxydo-réduction, présente un cycle annuel marqué dans le lac Oneida (New York). On a utilisé différentes méthodes pour mesurer, tout au long de l'année, les flux de Mn(II) provenant des sédiments : 1) des estimations fondées sur les changements des profils de l'eau interstitielle, 2) des mesures directes au moyen de chambres de flux in situ, 3) des gradients de concentration dans l'interface sédiment–eau dans des carottes incubées en laboratoire et 4) des changements dans les inventaires de manganèse hypolimnétique au cours de la stratification. Dans des bassins profonds du lac, des taux élevés de réduction du Mn(IV), jusqu'à 2,1 $mmol \cdot m^{-2} \cdot jour^{-1}$, ont été observés en été et au début de l'automne, avec une faible réduction pendant le reste de l'année. Dans les zones peu profondes du lac, où l'on trouve fréquemment des nodules et des croûtes de ferromanganèse, on a observé peu ou pas de réduction pendant l'année. Le cycle du manganèse est étroitement associé au cycle du carbone, d'après nos résultats, et joue un rôle important dans l'oxydation du carbone organique dans le lac, dérivée de la production photosynthétique élevée et de l'effondrement de la biomasse qui atteint l'interface sédiment–eau. Des expériences préliminaires avec des témoins empoisonnés semblent indiquer que la réduction du Mn(IV) résulte d'une combinaison de processus biologiques et abiologiques.

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Geochemical cycling of manganese in aquatic systems is controlled by many factors, most of which are intimately related to redox transformations occurring between the reduced, soluble (Mn(II)) and oxidized, colloidal, or particulate manganese phases (Mn(III), Mn(IV) (Stumm and Morgan 1981). In aquatic systems with stable oxic–anoxic interfaces, such as sediments or stratified water columns, the reduction of manganese oxides can lead to high concentrations of reduced manganese. Such high concentrations result in diffusion-driven manganese flux into the overlying waters. The resulting Mn(II) can then be rapidly returned to the surface sediments upon its reoxidation in the presence of oxygen, establishing the redox interface-dependent manganese cycle (Davison and Woof 1984).

The reductive part of these cycles is dependent on and closely linked to the input of organic carbon to the system. In fact, Mn(IV) reduction can account for a major percentage of carbon oxidation in some environments (Aller and Benninger 1981), through the mediation of both direct and indirect, biological as well as abiological mechanisms (Nealson et al. 1988). It is important to recognize and quantify the mechanisms that couple metal reduction to carbon oxidation in order to better understand manganese cycling in the aquatic environment. Only recently have heterotrophic bacteria been shown to utilize manganese (and iron) oxides directly as terminal electron acceptors (Lovley and Phillips 1988; Myers and Nealson 1988) and hence figure significantly in the fate of sedimentary organic carbon. Some of the organic carbon compounds used by these organisms are those commonly identified as the end products of fermentation, suggesting that consortia might be operating to break down the rich phytoplankton organic carbon via fermentation and to then oxidize these end products to CO_2 via dissimilatory metal reduction. Indirect mechanisms mediated by

[1]Present address: Carnegie Institution of Washington, Geophysical Laboratory, 5251 Broad Branch Road NW, Washington, DC 20015, USA, and the University of North Carolina at Chapel Hill, Chapel Hill, NC 27514, USA.

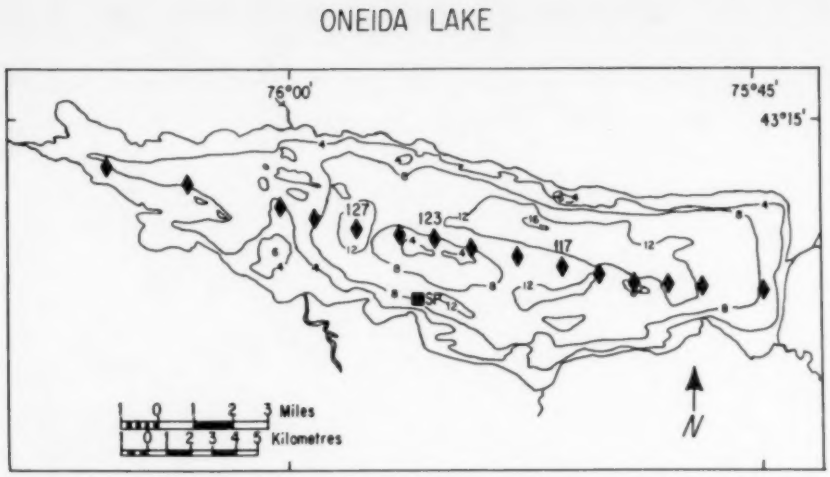

FIG. 1. Map of Oneida Lake. The solid diamonds represent the Barge Canal buoy line. Samples were collected at Buoys 127 and 123. The solid square represents station Shackelton Point (SP).

both organic and inorganic reducing compounds (Stumm and Morgan 1981), which in some cases are products of microbial activities, can be an important component in the reduction of manganese oxides (Stone 1987a, 1987b; Myers and Nealson 1988; Nealson and Myers 1992). Understanding the pathways and mechanisms that couple carbon oxidation to metal reduction is clearly prerequisite to understanding carbon diagenesis in environments with high metal concentration as described by Froelich et al. (1979).

To investigate pathways and mechanisms that influence metal reduction, we first had to document seasonal concentrations of manganese at various depths in the water column and sediments. Based on this information, manganese fluxes were estimated. In this study, several methods to measure soluble manganese flux were used ((1) porewater gradients, (2) flux chambers, (3) time course experiments with cores incubated in the laboratory, and (4) hypolimnetic concentration change) to examine the reductive component of the manganese cycle in Oneida Lake. Finally, we investigated the relative importance of biotic versus abiotic manganese reduction in sediments. Based on these results, we have proposed an annual cycle of manganese in Oneida Lake and estimated the importance of metal reduction to the oxidation of organic matter in the lake.

Methods

Field Site Description

Oneida Lake (Fig. 1) is located in the Ontario lowlands of central New York state, 16 km northeast of Syracuse (latitude 43°12.5′N, longitude 75°55′W). The lake is shallow with a mean depth of 6.8 m and maximum depth of 16.8 m (Greeson 1971; Mills et al. 1978). The lake contains permanent buoys (Fig. 1) which are markers of the New York barge canal system. These are located in the middle along the long axis and mark several shallow oxic areas (Buoy 123) and deep, potentially anoxic areas (Buoy 127) that have been used as sample locations for this work. Another station sampled was Shackelton Point (SP).

Oneida Lake is a model manganese-rich environment. It is a eutrophic, well-mixed lake with some periods of stratification present under low wind conditions. Seasonally high levels of primary production result in a substantial organic carbon sedimentation (Hansen and Blackburn 1992). Furthermore, high levels of manganese are present in and on the sediments as ferromanganese nodules and crusts. The lake exhibits two functionally different areas: (1) deep basins (depositional zones), in which sedimentation is rapid and extensive (Moore 1981), and (2) shallow basins (nondepositional zones) where there is little or no accumulation (Fig. 2). The major continuous oxic–anoxic interfaces in Oneida occur at the sediment–water interface in the deep areas of the lake and deeper in the sediments in other areas.

Oneida Lake's exposure to prevailing winds is of great importance in the dynamics of the lake and cycling of manganese. The lake is 33.6 km long and 8.8 km wide, with the long axis oriented west–northwest to east–southeast, being exposed to the prevailing winds, a factor that can determine mixing or stratified conditions. Wind speed and direction data were obtained from a NOAA weather station at the Hancock Airport in Syracuse, New York, which monitors meteorological parameters at hourly intervals. Sedimentation rates in depositional areas of the lake are 2.3 $mm \cdot yr^{-1}$ (Moore et al. 1980; Moore 1981). Nodule-rich areas do not have the fine-grained sediment characteristic of the deep sections of the lake, probably because of lateral transport of the sediments away from the shallow areas by strong currents. Nondepositional areas are characterized by extensive deposits of manganese in the form of ferromanganese nodules and crusts. The manganese to iron ratio in freshly precipitated deposits and in nodules is the range of 2.7–3.8 (Moore 1981). The high manganese content of the nodules in relation to iron makes them crumbly (Calvert and Price 1977).

Sampling

Water samples

Samples were taken at 1-m intervals throughout the water column with a prerinsed 5-L Van Dorn bottle. Water was collected at three main stations, 117, 123 and 127 (Fig. 1), with depths of 12.5, 8.5, and 12.5 m, respectively, and dispensed into 3-L acid-washed polycarbonate bottles. The

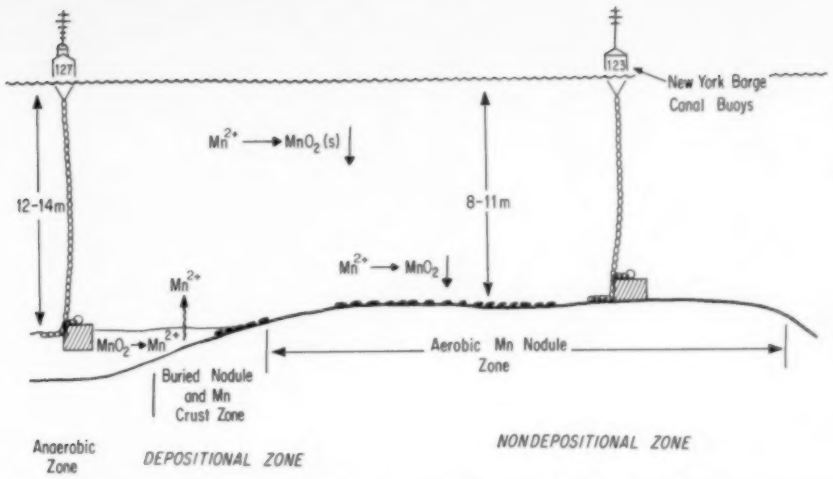

FIG. 2. Diagram of the two main areas in the lake, the depositional and nondepositional zones. In the potentially anoxic depositional zones (deep areas, e.g., Buoy 127), soluble manganese diffusion occurs when a stable thermocline is formed whereas nondepositional zones (shallow areas, e.g., Buoy 123) are always oxic and are characterized by the presence of ferromanganese nodules.

results presented in this paper are from a shallow station (123), located in the aerobic nodule-rich area, and station 117 for data in 1986 and from the added station 127 (depositional zone on the west side of the lake), located in the deeper area, for 1987 and 1988 (Fig. 1).

Supporting parameters such as pH (pH units), oxygen (micromoles per litre), temperature (degrees Celsius), and depth (metres) were measured. pH was measured with a Beckman Zeromatic SS-3 pH meter; oxygen concentration was obtained by the Winkler method, with samples fixed immediately (Wetzel and Likens 1991); a 400 Series Yellowspring Instruments (YSI) telethermometer was used to measure the water temperature in situ, with metre intervals marked for depth measurements. In 1987, a Datasonde II (Hydrolab Corporation) was acquired and was used to measure the support parameters. Samples were taken at different times during 1986–89 including under the ice in February, as soon as ice-out occurred in April, and during the summer and fall at 1-wk intervals. Bottom samples were taken 0.5 m above the bottom to avoid suspended sediment particles in the water samples. Samples from under the ice were taken at station Shackelton Point, with a depth of 12.5 m (Fig. 1). A hole was made through the ice and samples were taken in the same fashion as the other water samples and were transported immediately to the onshore laboratory at the Cornell Field Station.

Manganese Analyses

Water column samples

Duplicate and triplicate casts from different masses of water were taken with a prerinsed 5-L Van Dorn bottle. Unfiltered samples for total manganese analysis were transferred from the sampling device directly into 100-mL acid-washed polypropylene bottles. In the soluble manganese analysis, 50 mL of lake water was filtered through a 0.2-μm pore size polycarbonate Nuclepore filter supported by an acid-washed polycarbonate filtering unit, which was rinsed three times with deionized water between filtrations. The filtrate was collected in acid-washed polypropylene bottles, and 50 μL of ultraclean concentrated nitric acid was added to both sets of samples to obtain a pH of 2 before storing at 4°C for later analysis. Syringes, filter holders, and sample bottles were soaked with 10% HCl and rinsed three times with distilled, deionized water before use.

Manganese analyses were made with a Video 12 atomic absorption spectrophotometer (Instrumentation Laboratory) using a flame or a graphite furnace detector, depending on the manganese concentration of the samples. Concentrations were determined with a five-point calibration curve. Calibration standards were prepared from Baker Instra-analyzed atomic spectral manganese standard stock solution, diluted with distilled, deionized water in acid-washed volumetric flasks. Each sample was run three times or until a 3% standard coefficient of variation was obtained.

Porewater Samples

Core processing

Sediment cores were collected either with a gravity corer or by hand by divers using long and short liners (6.5-cm inner diameter and 46 cm long) acid washed and rinsed thoroughly before use. Cores were sectioned at 1-cm intervals in a glove bag with a nitrogen atmosphere (the February core was air-sectioned). Subsamples from the different sections were centrifuged in 1.5-mL centrifuge tubes at 4000 rpm for 15 min in an Eppendorf Centrifuge 5415. Porewater was then filtered through a 0.2-μm Nuclepore filter and acidified with ultraclean nitric acid to pH 2 and stored in a refrigerator until analyzed.

During August 1988, a second set of samples was taken in order to compare air-sectioned versus squeezed sediment cores. In the latter, porewater was obtained with a squeezer, similar to the whole core squeezer described by (Jahnke 1988). For this method, porewater concentrations of manganese were measured at 1-cm intervals. Porewater was collected directly into gas-tight syringes connected to the ports via luer fittings. To facilitate flow of porewater, a 6.5-cm

length of 1/8-in.-diameter porous (70 μm) polyethylene rod was inserted through the luer fitting. Porewater was then acidified and kept in a refrigerator prior to analysis. Samples were also taken for measuring porosity of the sediments for flux calculations.

Flux Calculations

(1) Porewater gradients

Fluxes of manganese were calculated from measured concentration gradients (from porewater profiles) at the sediment–water interface via Fick's first law of diffusion (Berner 1980):

$$J = D_S \phi \, dC/dz$$

where J is the flux of soluble manganese, D_S is the sediment diffusivity of manganese taken from Li and Gregory (1974), ϕ is the porosity at the sediment–water interface, and dC/dz is the slope of the concentration gradient at the sediment–water interface. Porosity was estimated from wet and dry weight measurements and included a correction for tortuosity, which results from the presence of particles. An ion is not free to diffuse as in the overlying water, but is hindered by collisions with the particles that form the sediment and therefore follows a tortuous path through the fluid between and around particles (Berner 1980). The tortuosity correction (Ullman and Aller 1982) assumed a density of 2.45 $g \cdot cm^{-3}$ for clay sediment (nondepositional zones) and 2.7 $g \cdot cm^{-3}$ for sandy sediments (depositional zones) of the lake. In freshwater sediments with different porosity such as Oneida Lake, the molecular diffusion coefficient at temperature can be used to calculate a reliable sediment diffusion coefficient (Sweerts et al. 1991b) from porewater measurements.

(2) Flux chambers

In situ manganese flux measurements were also made via flux chambers. The chambers were polypropylene bottles fitted with an outside rim so that when they were inserted into the soft sediments, 18 L of bottom water was enclosed. Prior to sampling, flux chambers were placed 10–15 cm into the sediments in different locations, at the bottom of the shallow and deep stations by divers. After 24-h equilibration period, a teflon stopper with a syringe needle was placed in the orifice, and samples were taken by divers with a 30-mL syringe at daily intervals. The water in the chambers was gently mixed prior to sampling by aspiration, and after the sample was removed, 30 mL of bottom water was added to the chamber to restore constant volume. Oxygen concentration (Winkler titration) and pH (minielectrode) were measured in each sample to monitor the changes within the chambers. Fluxes were calculated by sampling the change in manganese concentration in the chamber with time, knowing both the surface area and total volume of water in the chamber. Samples were then taken to the laboratory, filtered through a 0.2-μm Nuclepore filter, acidified, and maintained at 4°C until analyzed.

(3) Flux measurements in laboratory-incubated cores

Dissolved manganese flux was also estimated by incubating whole cores in the laboratory using a procedure similar to the one described by Sweerts et al. (1991a). Cores were collected with a gravity corer, sealed with tight plastic caps in order to minimize oxygen exchange, and returned to the onshore laboratory. Once in the laboratory, the overlying water (approximately 0.38 L) was deoxygenated with nitrogen. A 5-mL sample was removed at 30-min intervals for Mn(II) analysis. Equal volumes of filtered, deaerated bottom water were added to replace the volume taken from the overlying water.

(4) Seasonal changes in hypolimnetic manganese inventories during stratification

Spatial and temporal changes in soluble manganese concentrations were measured and concentration profiles were obtained from these data. Manganese flux from the sediments into the hypolimnion could then be estimated by comparing temporal changes in these profiles. This could only be done when calm weather allowed a stable thermocline and anoxic conditions to prevail. The details of the method can be found in Aguilar (1992). Data from a depositional zone were used in 1988.

Biotic versus Abiotic Manganese Reduction in Sediments

$^{54}MnO_2$ reduction experiments were conducted in order to elucidate the contribution of biotic (nonpoisoned) versus the abiotic, chemical (poisoned samples) Mn(IV) reduction. Mercuric chloride ($HgCl_2$) has been shown to inhibit biological activity and to have a minimal effect on the manganese chemistry at the concentration and pH used (Rosson et al. 1984), and therefore, it is an effective inhibitor of biological manganese reduction. This method was convenient and unambiguous in addressing depth-specific processes in the sediment and discriminating between biotic and abiotic processes whereas rates were more effectively established by the other methods (e.g., porewater gradients, etc.). Slurries can be mixed after adding the inhibitor and be more effective than in whole sediment cores, where diffusion might be slower and adsorption to the sediment may make the poison unavailable.

Experiments to elucidate the nature of the reduction were performed with sediment collected in April 1988 from station 127. The core was sectioned and put into polycarbonate acid-washed containers, gassed with nitrogen, and transported cold (4°C) and dark. Core sections were kept under the same conditions in the laboratory until radiolabel experiments were performed in early May. Another set of experiments was performed from a core taken September 9, 1990, at station 127. The samples were treated and transported the same as in April. Radiolabel experiments were performed in the laboratory starting September 11, 1990.

The experiment from the core collected in April utilized $HgCl_2$ at a final concentration of 100 μM and manganese was added at 250 μCi (1 μCi = 37 kBq) of $^{54}MnO_2$, prepared according to Burdige and Nealson (1985, 1986). The slurries were prepared by adding 2 mL of the sediment slurry from the 0–1 cm depth interval (mixed 1:1, w/w, with deoxygenerated water) to 200 mL of filtered deoxygenated Oneida Lake bottom water collected in April. The 0–1 cm interval was sectioned and maintained under nitrogen throughout the different manipulations. Slurry samples were then added to polypropylene bottles, always under nitrogen; $HgCl_2$ was added to the slurries in 1 h before adding the tracer. These incubations were maintained at 4°C. After tracer addition, samples were taken at different time intervals to document the appearance of labeled soluble (reduced) manganese.

In the experiment performed in September 1990, $HgCl_2$ was used at 500 μM final concentration; all treatments were made in triplicate and different depth intervals were used

in the experiment (0–1, 1–3, 3–6, and 6–10 cm). The slurries were made by adding the same weight of bottom water (sparged with nitrogen) to sediment. Then, 10 mL of the slurry was combined with 90 mL of deoxygenated bottom lake water from the deep station in polypropylene bottles. After adding the $HgCl_2$ and allowing it to equilibrate at least 1 h, 250 μCi of $^{54}MnO_2$ was added to the different containers. In this experiment, samples were incubated at room temperature (18°C) in a Coy anaerobic chamber (Coy Laboratory Products, Ann Arbor, Mich.) with an atmosphere of 10% hydrogen plus 90% nitrogen as previously described (Myers and Nealson 1988). All sample containers were sparged with nitrogen throughout the manipulations before being put into the anaerobic chamber.

The scheme used to separate the different samples (i.e., adsorbed, reduced, and oxidized manganese) is shown in Fig. 3. A 5-mL sample was taken from each incubation container and filtered through a 0.2-μm Nuclepore filter in a Millipore filtering manifold. The sediment was then incubated with 5 mL of 10 mM copper sulfate for 30 min (to remove any reduced Mn(II) adsorbed to the sediment or to the manganese oxide). This was then filtered and the initial filtrate plus the copper wash were combined to give the reduced manganese fraction. The sediment sample still in the filter was then treated for 5 min with 5 mL of 0.5% hydroxylamine (to reduce any remaining manganese oxides) and filtered to give the unreduced manganese (manganese oxide). The remaining counts represented the filter-bound manganese. Totals were taken directly from the polypropylene bottles and experimental totals were obtained by adding the different components. Samples were counted in a Packard auto-gamma 5002 counter.

Results

The establishment of the thermocline was an important event that led to the development of anaerobic conditions in the hypolimnetic waters (observed in depositional zones) and subsequently allowed diffusion of soluble manganese from sediments into the hypolimnion. Even when high levels of Mn(II) accumulated in the deep zones of the lake, the shallow zones exhibited one sixth or less of the dissolved manganese concentration. This increase was not observed in surface waters; high concentrations of Mn(II) were restricted to the hypolimnion.

Deep Station (Buoy 127, Depositional Zone)

Protracted thermal stratification was observed only during 1986 and 1988. In each of the three years of study, surface water temperature showed a similar temporal pattern: a steady increase from ice-out in mid-April until each June when the temperature fluctuated around 20°C, reaching a maximum of about 27°C late in the summer (Fig. 4A). Similar temperature changes were seen throughout the surface waters of Oneida Lake. Temperature in deep areas (12 m) showed an increase after ice-out, although warming was less rapid than that seen at the surface, so that by the end of spring and beginning of the summer, isothermal conditions no longer existed. During midsummer months in 1986 and 1988, after periods of warm and calm weather, surface and deep temperatures differed by as much as 10°C, indicative of the formation of a thermocline that lasted almost 1 mo in the former year and almost 2 mo in the latter. During 1987, the temperature difference between surface and bottom was much less than in the other two years due to wind-driven mixing during the summer; hypolimnetic anoxic conditions were also absent during the summer of 1987.

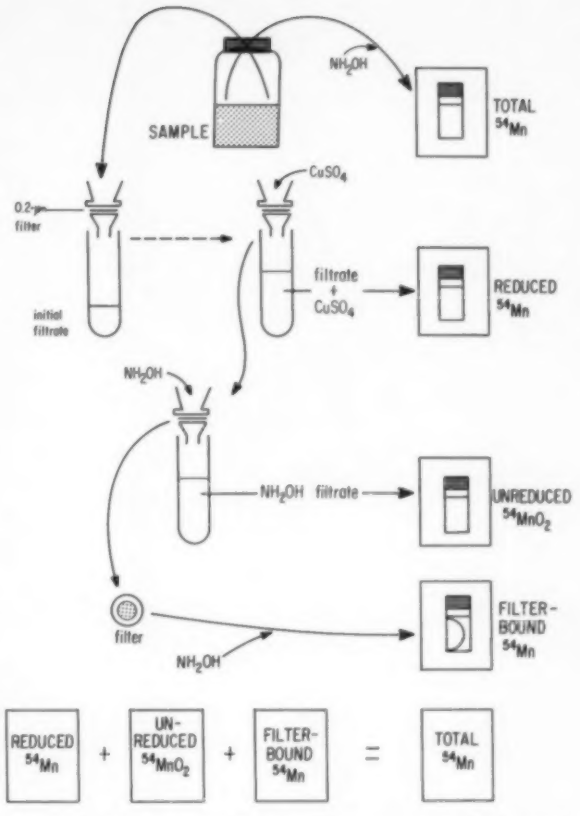

FIG. 3. Scheme to separate different components in the manganese reduction slurry experiments where $^{54}MnO_2$ was added. These components included total activity, reduced manganese (10 mM copper wash), unreduced manganese (0.5% hydroxylamine wash), and filter-bound ^{54}Mn in each sample.

During the winter and early spring, the water column was oxygenated throughout (Fig. 4B). Oxygen concentrations in the surface waters were high throughout the year, where values of approximately 300 μM were observed until late in the year. A decline in the oxygen concentrations in the bottom waters was observed during the summer months when low oxygen values were correlated with the onset of the thermocline. As a result, oxygen concentrations remained low during July and early August, establishing a suboxic hypolimnion. Extended stratification was a prerequisite for oxygen depletion during both 1986 and 1988. When hypolimnetic oxygen concentrations were low for long periods of time (Fig. 4B), oxygen values were approximately zero (<5 μM). During 1987, the lowest oxygen concentration observed was 55 μM, since the thermocline was not stable due to the wind-driven mixing. For all three years, wind mixing occurred in September and the thermocline was dissipated, resulting in a uniform distribution of oxygen throughout the water column. Thus the onset and duration of the anoxic conditions in Oneida Lake varied depending on local winds.

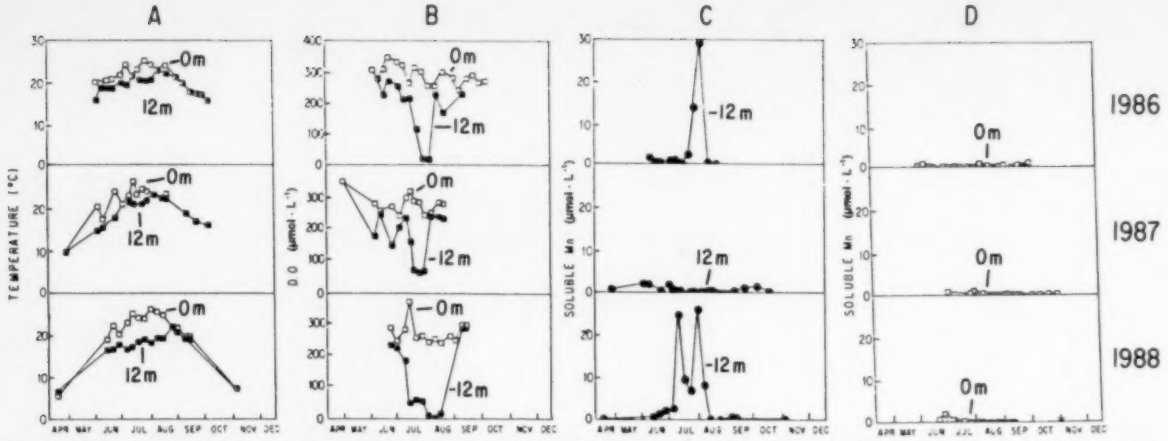

FIG. 4. Parameters from the depositional zone, deep station 127, 1986–88: surface (open symbols) and bottom (solid symbols). (A) Temperature; (B) dissolved oxygen; (C) dissolved manganese at depth (12 m); (D) dissolved manganese in surface waters.

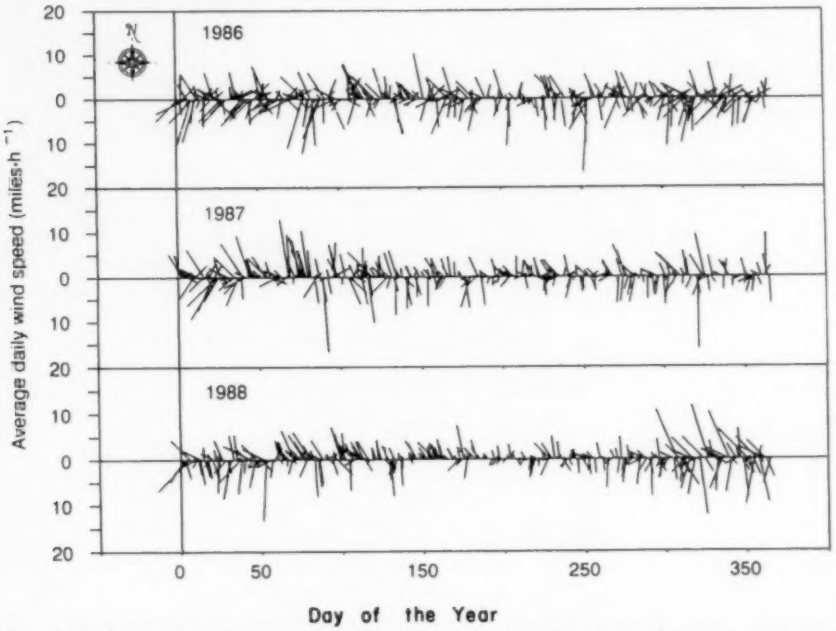

FIG. 5. Wind speed and direction from local climatological data, Hancock Airport, Syracuse, N.Y., 1986–88.

Hypolimnetic oxygen depletion led to the flux of soluble manganese into bottom waters in depositional zones. Soluble manganese concentrations in hypolimnetic waters showed considerable variation within the years of this study (Fig. 4C). Soluble manganese accumulated in deep stations when thermal stratification and low oxygen concentrations prevailed. This was observed in two (1986 and 1988) of the three years by the measured increase in hypolimnetic dissolved manganese concentration. Areas with a depth of approximately 12 m exhibited an increase in manganese concentration to about 30 μM in 1986 and 1988, values that were consistent with data from other deep stations sampled during the time. In 1987, this increase was not evident in the hypolimnion, and dissolved manganese concentration was much lower, approximately 0.5 μM. During 1987, when dissolved oxygen remained at 60 μM or above, dissolved manganese reached a maximum of only 1 μM or less.

Soluble manganese released from the sediment was largely confined to the hypolimnion, while epilimnetic concentrations of soluble manganese remained lower. During the three years of our study, dissolved manganese concentrations in the surface waters exhibited an entirely different pattern from the hypolimnetic manganese. Soluble manganese concentrations in surface waters (Fig. 4D) were consistently low throughout the year, approximately 0.5 μM. When mixing occurred, manganese concentration increased to 1 μM (Fig. 4D). The epilimnetic dissolved manganese concentrations throughout the lake were similar to those of the streams in the drainage

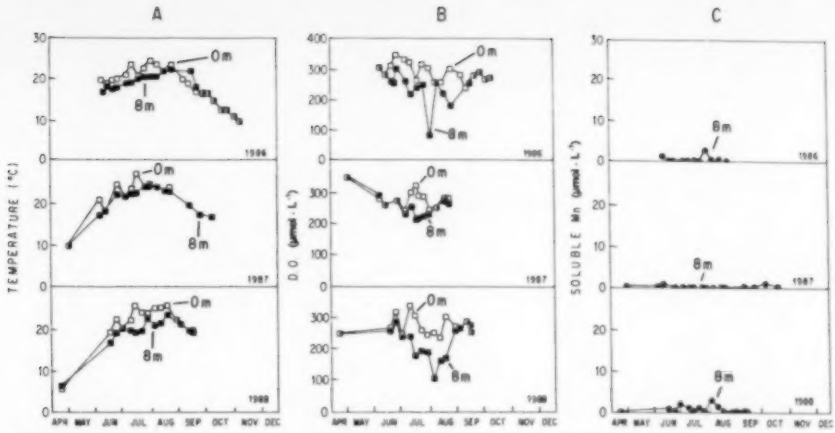

FIG. 6. Parameters from a nondepositional zone, shallow station 123, 1986–88: surface (open symbols) and bottom (solid symbols). (A) Temperature; (B) dissolved oxygen; (C) dissolved manganese at depth (8 m).

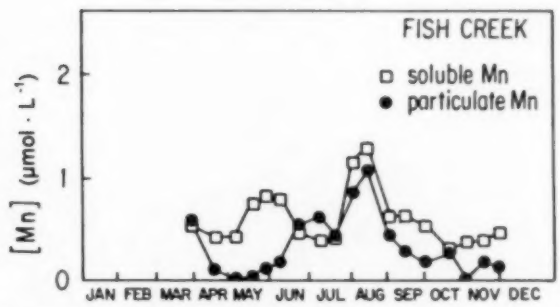

FIG. 7. Concentrations of soluble (open symbols) and particulate (solid symbols) manganese in Fish Creek, the main tributary which represents 44% of the total inflow to Oneida Lake.

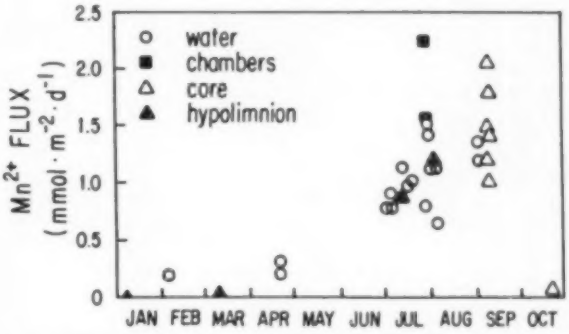

FIG. 8. Manganese flux data in different months, based on porewater profiles (open circles), measured with a flux chamber (solid squares), measured from incubated cores in the laboratory (open triangles), based on changes in hypolimnetic manganese inventories during stratification (solid triangles).

basin of Oneida Lake. The concentration fluctuated only slightly throughout the year, with a maximum manganese concentration of approximately 1.5 μM observed during 1988.

Wind-mixing events were an important component in determining the presence or absence of a stable thermocline during the summer months. The prolonged presence of a thermocline was a prerequisite for oxygen depletion in the hypolimnion, which led to flux of soluble manganese and its accumulation in the bottom waters. Wind patterns for the three years show that during 1986 and 1988, there were periods of calm weather where wind was not strong whereas in 1987, wind was a factor in maintaining a well-mixed water column (Fig. 5).

Shallow Station (Buoy 123, Nondepositional Zone)

Surface temperatures showed a similar pattern during each of the three years of our study in both the deep and shallow areas. Temperature increased from ice-out in mid-April to early May when it reached 20°C; summer surface temperatures fluctuated around 22°C (Fig. 6A). Temperatures at the bottom were very similar to those at the surface, although slightly cooler bottom waters were observed during summer months. No thermocline was observed in nondepositional areas.

In contrast with station 127, shallow areas were not conducive to the release of manganese from the sediments, since oxygen concentrations in bottom contact water were always high and sediment accumulation was low. Oxygen concentrations at the surface were similar during the three years (Fig. 6B), approximately 300 μM, and while some episodically low oxygen excursions were noted at 8 m depth, no truly anoxic conditions were observed. During 1986, oxygen at a depth of 8 m remained high, around 200 μM, and had a lowest value of approximately 80 μM in early July. During 1987, oxygen at the bottom was approximately 200 μM. In 1988, oxygen concentrations fluctuated between 100 and 150 μM.

In general, dissolved manganese concentrations at the bottom of the shallow station remained low except for an increase to approximately 2 μM during midsummer in both 1986 and 1988 (Fig. 6C). These changes were concurrent with high concentrations of dissolved manganese in deeper parts of the lake during the same period (Fig. 4C). In 1988, there were several events at Buoy 127 in which dissolved manganese increases were seen at depths as shallow as approximately 6 m (Fig. 4C). During these periods, a slight

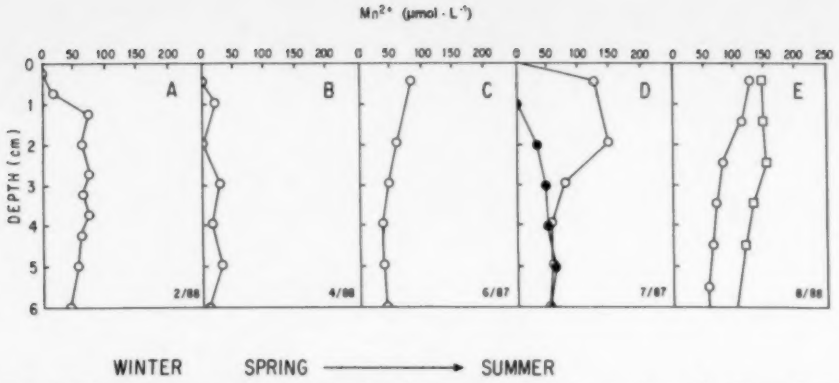

FIG. 9. Dissolved manganese concentrations in porewater from the top 6 cm of sediment from depositional zones (open circles). Winter to summer changes are represented by the five samples (A–E) from either 1987 or 1988. (A) Under the ice at station Shackelton Point; (B) in April after ice-out at station 127; (C) June at station 127; (D) July at station 127 (open circles) and a nondepositional zone, station 123 (solid circles); (D) August at station 127 from a centrifuged core (open circles) and a squeezed core (open squares). Standard error was smaller than the symbols.

increase (approximately 2 μM) was observed in the shallow areas and correlated with the high flux events in the hypolimnion of deep areas of the lake.

Much of the activity of the manganese cycle occurred in the hypolimnetic waters (6–12 m) due to flux of dissolved manganese from the sediment, which probably occurred continuously during the summer. Manganese was present in the hypolimnion due in part to thermal stratification during mid-July and early August and low oxygen concentrations in the bottom waters. This pattern was observed in the deep stations and even when strong reductive events occurred in these areas, manganese concentration observed in the shoals was not as high as in deeper areas.

These data not only indicate that the sediments of the deep zones are the source of high soluble manganese concentrations seen in hypolimnetic waters during the summer months, but also that the manganese cycle for the lake is tightly coupled to internal cycles. Analyses of different tributaries were undertaken to measure the input of soluble and particulate manganese to the lake. Soluble manganese in the hypolimnion cannot be accounted for by external inputs alone. The approximate volume of deep hypolimnetic zones is 30% of the total lake volume. In order for the rapid increase in hypolimnetic manganese to be driven by external sources (i.e., riverine input), manganese from rivers would have to enter the lake at very high concentrations, inconsistent with our observations (the turnover time for the lake is 235 d). The major tributary, Fish Creek, supplies about 44% of the total inflow to Oneida Lake (Greeson 1971), and soluble manganese concentrations fluctuate from very low to approximately 1.2 μM during mid-July (total manganese concentration at this time was approximately 2 μM) (Fig. 7). These values are similar to those of all other tributaries to Oneida Lake (Aguilar 1992). These external concentrations are not sufficient to explain the large and dynamic increase seen in hypolimnetic waters of the lake.

Flux Estimates

(1) Porewater gradients

Dissolved manganese flux was calculated based on porewater profiles of dissolved manganese from different cores taken during the summer from the deep station 127 area (Fig. 8, open circles). Values from winter and spring were lowest, approximately 0.200 $mmol \cdot m^{-2} \cdot d^{-1}$, and increasing flux was observed with time until the end of the summer, when the highest value obtained through this calculation was 1.38 $mmol \cdot m^{-2} \cdot d^{-1}$. Because little sediment accumulates in the oxic zone, it was not possible to obtain similar profiles from the hard clays in the shallow station. However, one core was processed from that area and yielded a flux of zero.

Porewater profiles of dissolved manganese showed distinct temporal patterns. During the winter when the lake was covered with ice (Fig. 9A), calculated fluxes indicated little or no reduction, with 0.18 $mmol \cdot m^{-2} \cdot d^{-1}$ released and a concentration at the oxic–anoxic interface of close to zero. During spring, after ice-out in April (Fig. 9B), flux from the sediments was still low (0.29 $mmol \cdot m^{-2} \cdot d^{-1}$), with maximum concentrations of only 30 μM at 5 cm depth, similar to the winter profiles.

In June, Mn(II) concentration profiles showed higher concentrations in the surface sediments, approximately 85 μM, and decreasing concentrations with depth. Below 4 cm the concentration was 35 μM. Calculated manganese flux increased from 0.192 in April to a value of 0.76 $mmol \cdot m^{-2} \cdot d^{-1}$ at the end of June (Fig. 9C). Also, by this time the temperature had increased significantly at the surface sediments (Fig. 4A).

In July, Mn(II) concentration in the top sediment was approximately 140 μM (Fig. 9D), with this concentration extending to a depth of 4 cm. At this time, flux of dissolved manganese was calculated to be 1.1 $mmol \cdot m^{-2} \cdot d^{-1}$. A comparison was made between the deep and shallow zones of the lake. The deep station showed a high manganese concentration at 0.5 cm whereas the core from the shallow zone (solid circles) increased in concentration to approximately 50 μM at 2 cm and showed no soluble manganese above that depth (Fig. 9D).

The August (Fig. 9E) soluble manganese porewater profiles were similar to those from July. The top concentration from the sectioned and centrifuged and squeezed samples

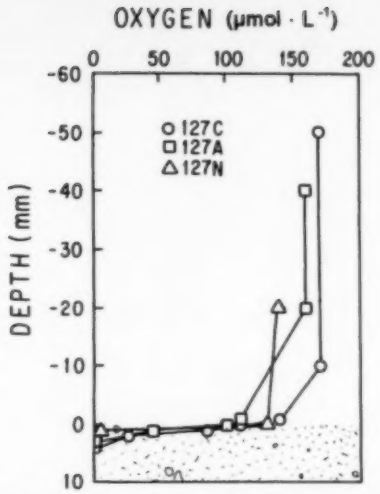

FIG. 10. Dissolved oxygen in porewater profiles from three cores collected at a depositional zone (station 127) during the summers of 1987(A), 1988 (N), and 1990 (C). Depth "zero" is the sediment–water interface; the stippled zone is the sediment.

was similar, so for these calculations, the measured porewater concentrations agreed adequately. There was a discrepancy in the overall comparison of the two profiles of approximately 50 μM, but this occurred below the concentration gradient, and so had no effect on the calculated fluxes of soluble manganese.

Oxygen concentration can be an important component in triggering manganese flux from the sediments into hypolimnetic waters. In general, oxygen is depleted in the top few millimetres of the sediment–water interface (Carlton et al. 1989). Oxygen concentration as well as pH were measured in sediments from the deep areas of the lake, from three cores taken in 1987 around Buoy 127 (Fig. 10); a pH of 8 was measured from surface to 8 cm with no change. Overlying water at 50 mm from the sediment was oxygenated with a concentration of approximately 160 μM and oxygen was high until the sediment–water interface was reached where the concentration dropped precipitously, reaching zero (undetectable by the microelectrode) at a depth of 3–4 mm from the interface. This short oxygen penetration in deep sediments can be due to microbial oxidation of reduced compounds at the sediment–water interface (Sweerts et al. 1991a). The pH values remained between 7.5 and 8 with depth, showing little variation throughout the summer. Even when oxygen is present in the hypolimnion (as in 1987), oxygen in the sediment reaches zero in the first 5 mm or less from the sediment–water interface.

(2) Flux chambers

Flux measurements of dissolved manganese were also performed using flux chambers (Fig. 8, solid squares) that were placed in the oxic and anoxic parts of the lake. These measurements ranged between the high end of the porewater measurements and the highest numbers calculated for dissolved manganese flux during the summer months, approximately 2.3 $mmol \cdot m^{-2} \cdot d^{-1}$. In the shallow zones, manganese flux was much lower than in deep zones, reaching only approximately 0.0024 $mmol \cdot m^{-2} \cdot d^{-1}$.

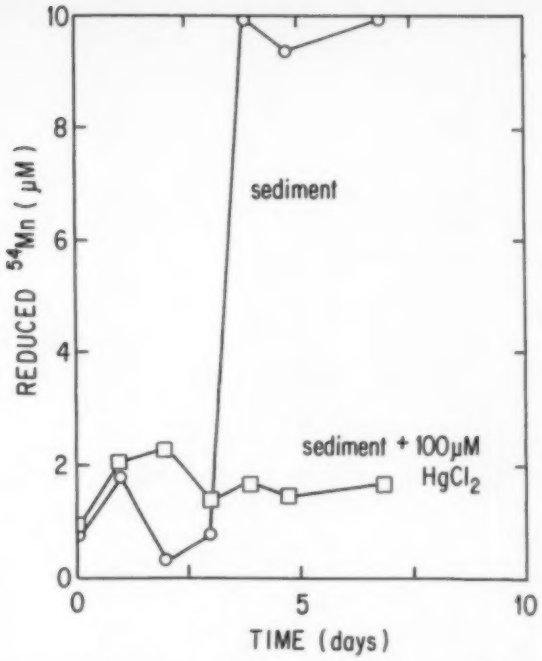

FIG. 11. Results from the slurry experiments with sediment collected in April 1988 showing reduction of $^{54}MnO_2$ from sediment (open circles) and sediment with 100 μM $HgCl_2$ added (open squares).

(3) Incubated cores

Fluxes were also measured in laboratory-incubated cores taken in September of 1990 at the deep station (127). From six cores, the calculated flux was consistent with the values obtained with porewater concentrations and ranged between 1.0 and 1.4 $mmol \cdot m^{-2} \cdot d^{-1}$ (Fig. 8, open triangles).

(4) Hypolimnetic manganese inventories during stratification

Fluxes based on hypolimnetic concentration changes (Fig. 8, solid triangles) during 1988 were consistent with other flux measurements for that period. This type of calculation is only possible when the thermocline is present and hypolimnetic dissolved manganese concentrations are high from 6 to 12 m depth (Aguilar 1992). These measurements were similar to the porewater results, establishing a 1.5 $mmol \cdot m^{-2} \cdot d^{-1}$ flux for the summer months. In the cases of flux chambers and incubated cores, the flux value was higher, approximately 2.3 $mmol \cdot m^{-2} \cdot d^{-1}$.

These flux estimates were made over a 3-yr period, and given the inherent variability of each method, they were remarkably consistent. Highest values were obtained by direct measurements with a flux chamber and are comparable with the highest manganese fluxes obtained in other aquatic systems using the same methods as in this study.

A seasonal change was thus evident in dissolved manganese flux (Fig. 8), where manganese flux was lower during winter and spring (0.19 $mmol \cdot m^{-2} \cdot d^{-1}$), showing an increasing trend during the summer, and then reaching a high flux (1.5–2.3 $mmol \cdot m^{-2} \cdot d^{-1}$). Thereafter, manganese flux in the fall showed a decreasing trend reaching the low

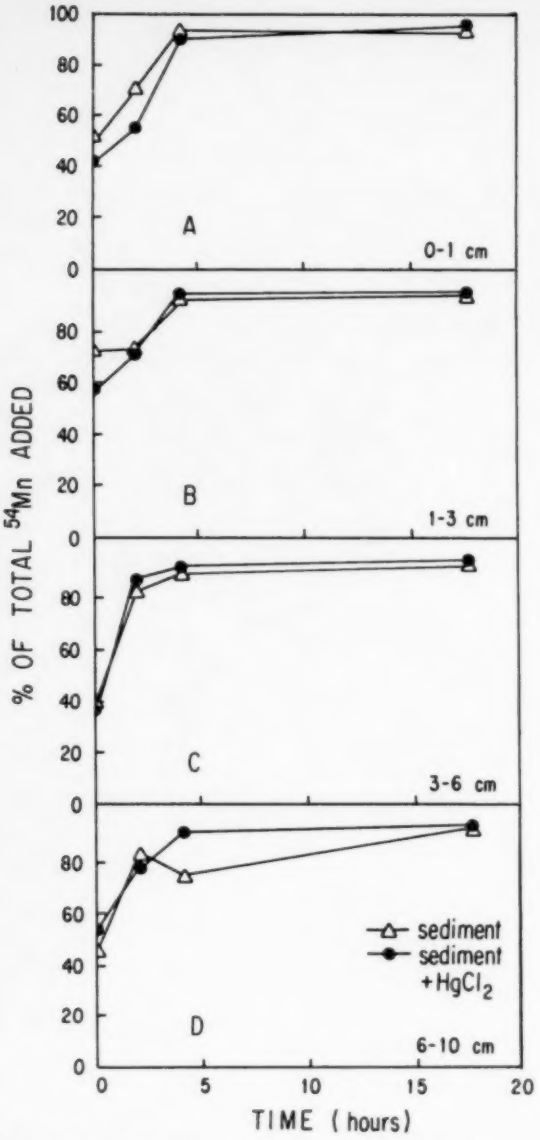

FIG. 12. Results from the slurry experiments with sediment collected in September 1990 showing the percentage of total reduction of $^{54}MnO_2$ added to the (A) 0–1, (B) 1–3, (C) 3–6, and (D) 6–0 cm sections from the sediment core. In all cases, open triangles represent untreated sediment and solid circles represent sediment with $HgCl_2$. Standard error of the triplcate samples was smaller than the symbols.

flux found during winter. This shows that the bulk of the manganese flux took place during the summer months and accounted for approximately 85% of the annual flux of dissolved manganese.

Biotic versus Abiotic Manganese Reduction in Sediments

$^{54}MnO_2$ reduction experiments were conducted to separate biological (nonpoisoned) from abiological ($HgCl_2$-poisoned) Mn(IV) reduction. Experiments performed with sediment collected in April 1988 from station 127 showed that manganese reduction was inhibited by $HgCl_2$. After 3 d the biotic sample (nonpoisoned) was completely reduced, while the abiotic sample (poisoned) showed little reduction (Fig. 11). In this experiment the sediment slurry was made using bottom water from station 127, containing approximately 30 μM NO_3. It is possible that the addition of nitrate to the sediments provided a better electron acceptor, resulting in a 3-d "lag" before manganese reduction resumed. Subsequently, manganese oxides were reduced quickly.

Sediment slurries from sediment collected at four depth intervals, 0–1, 1–3, 3–6, and 6–10 cm, at station 127 were used for the second reduction experiments with $^{54}MnO_2$ (September 1990). In the 0–1 cm interval the initial point in the experimental sample had 50% reduction and increased until approximately 4 h when all the added manganese was reduced (Fig. 12). A similar progression was observed in the 1–3 cm interval where in the poison control, 40% of the manganese was reduced in a short time. After 3 h, both the experimental and control had the same rate of reduction. In the 3–6 and 6–10 cm intervals, both the experimental and the poison control had the same type of curve and both showed a similar pattern of reduction. These data indicated a very large difference between the early summer and late fall sediment characteristics, the former showing primarily biologically mediated Mn(IV) reduction after 3 d and the latter appearing to be primarily abiotic due to reducing conditions in the sediments.

During September 1990 and after the summer activity, sediments were highly reducing. Below 1 cm depth, chemical reduction processes had an impact in the reduction patterns of the sediment. Dissolved iron influences the redox behavior of manganese: under anoxic conditions, iron reduces manganese oxides (Myers and Nealson 1988). It is possible that part of the increase in dissolved manganese concentrations in the sediments is due to the chemical reduction of manganese oxides in the presence of reduced iron. Dissolved iron concentrations found in the sediments were usually less than half the concentration for dissolved manganese, and so at best offer a partial explanation.

These experiments were designed to investigate the biotic or abiotic nature of manganese reduction in the sediments of Oneida Lake. Differences in the reducing conditions of the sediments allow only a general conclusion; a definitive explanation awaits more comprehensive experiments in different areas of the lake throughout the year.

Discussion

The flux of soluble manganese from the sediments to hypolimnetic waters of Oneida Lake, New York, exhibits considerable temporal and spatial variation within and among years. During the winter when the lake is covered with ice and just after the first mixing of the year after ice-out, manganese flux is very small and starts to increase in June. The increase in Mn(II) concentration is observed until it reaches its highest value during midsummer, decreasing again during the fall to a low value. There is definite seasonal factor in the manganese flux from the sediments to the overlying waters that involves the onset of a thermocline. When a thermocline is established, anoxic conditions are present, and therefore, high manganese concentrations (20–30 μM) can be

TABLE 1. Dissolved manganese flux in Oneida Lake, New York, measured by four different methods, with examples from other aquatic environments.

Mn(II) flux (mmol·m22·d21)	Location	Source
	Porewater gradient	
0.003	Oneida Lake (shallow zone)	This study
0.019	Lake Baikal	Klumpa
0.09	Gullmars Fjord	Sundby et al. 1986
0.18	Oneida Lake, winter (deep zone)	This study
0.19	Lake Washington	Murray 1987
0.19–0.25	Green Bay	Klumpa
1.38	Oneida Lake, summer (deep zone)	This study
	Flux chamber	
0.005	Oneida Lake (shallow zone)	This study
0.05–0.41	Narrangansett Bay	Hunt 1983
0.37	Lake Washington	Murray 1987
1.4–2.1	Oneida Lake (deep zone)	This study
	Mass balance	
0.11	Lake Washington	Murray 1987
	Hypolimnetic concentration change	
0.89–1.2	Oneida Lake (deep zone)	This study
	Incubated cores	
1.0–1.4	Oneida Lake (deep zone)	This study

[a]From Dr. J. Val Klump (Center for Great Lakes Studies, 600 E. Greenfield Ave., Milwaukee, WL 53204, USA, personal communication).

observed from the bottom up to a depth of 6 m (the bottom of the metalimnion).

Depositional zones of the lake are the source of the high hypolimnetic soluble manganese observed during the summer months. This and the fact that soluble manganese input concentrations from tributaries are much lower than those observed in hypolimnetic waters show that the manganese cycle in Oneida Lake is primarily internal. As demonstrated by the abundant manganese nodules, there is net accumulation of particulate manganese in nodules and crusts in the aerobic shoal areas of the lake.

The results from flux measurements indicate that vigorous reduction of manganese occurs during the summer and early fall, resulting in large fluxes of Mn(II) out of the sediments. These fluxes, which are among the highest reported (Table 1), are confined to a short period of time during the year, consistent with a recent model developed by Johnson et al. (1991) which predicts a pattern virtually identical to that measured during this study. Net accumulation in the water column occurs only during rare periods of stratification. During mixing, the reoxidation of the manganese is apparently rapid and complete.

The high dissolved manganese fluxes observed reflect the eutrophic characteristics of Oneida Lake and its active manganese cycle. This intense activity may have several origins. Temperature increase of the bottom waters occurs rapidly during the summer months and probably increases microbially mediated rates during that time. Also the formation of a stable thermocline and the onset of anoxic conditions in the hypolimnion allow the soluble manganese to be present in the bottom waters.

Due to the eutrophic nature and shallowness of the lake, a large amount of labile organic matter from different blooms can deposit rapidly. A major component remains undecomposed and is therefore available for further decomposition at the sediment–water interface. This increases oxygen consumption, thereby stimulating anaerobic processes and mineralization, causing increased concentrations of reduced dissolved chemical species (Hansen and Blackburn 1992). High photosynthetic rates in the surface waters provide a large amount of carbon to support the carbon and other electron acceptor needs of microorganisms present in the sediment. Within certain eukaryotic algae, decomposition starts within the first days and soluble compounds increase rapidly (Mills and Alexander 1974).

Certain species of cyanobacteria, such as *Aphanizomenon* sp. and *Anabaena* sp., are susceptible to mineralization whereas *Microcystis* sp. is less susceptible (Fallon and Brock 1979), so this species can still be present after long periods of time. All of these species are present as high biomass components during the summer in Oneida Lake (Dean and Greeson 1979). Therefore the supply of carbon and other elements from the phytoplankton in the epilimnion is to some degree predictable, and different stages of mineralization can be found depending on the nature of the epilimnetic phytoplankton composition. The extent of accumulation of organic matter into the sediments depends on bottom currents. In the shallow nondepositional areas in the

middle of the lake, virtually no accumulation occurs whereas in the deep depositional areas, there is a net accumulation every year.

Flux measurements are relevant for understanding the manganese cycle and its relationship to the carbon cycle, since the flux of Mn(II) can be related to oxidation of organic carbon via the Redfield equation (Froelich et al.1979):

$$(CH_2O)_{106}\,(NH_3)_{16}\,(H_3PO_4) + 236\,MnO_2 + 472\,H^+$$

$$\rightarrow 236\,Mn^{2+} + 106\,CO_2 + 8N_2 + H_3PO_4 + 366\,H_2O.$$

As a result of such reductive processes, the reduced form of manganese is produced in the sediments, accumulated in the porewaters, and then diffused into the water column. when a stable hypolimnion is present, Mn(II) concentration in the hypolimnetic waters increases due to diffusion, as was the case for the soluble manganese during the summer. In Oneida Lake, we estimated that manganese reduction alone accounted for the oxidation of approximately 3.6% of the total carbon fixed in 1987 and approximately 5% in 1988 (Aguilar 1992).

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Life History Forms of Male Masu Salmon (*Oncorhynchus masou*) in South Primor'e, Russia

V.V. Tsiger, V.I. Skirin, N.I. Krupyanko, K.A. Kashkin, and A.Yu. Semenchenko

Pacific Research Institute of Fisheries and Oceanography (TINRO), Vladivostok, Russia

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In South Primor'e (Russia), mature male masu salmon (*Oncorhynchus masou*) parr are found at age 0+ to 3+ (9–22 cm). After first maturation, some male parr die, while others survive and mature the following year. Immature males become smolts after one or two winters in rivers and migrate to the sea in spring – early summer. After one winter in the sea, they return as sea-run normal-sized (40–70 cm) males at age *R*.1+. Besides mature male parr and normal-sized sea-run males, jacks (28–33 cm) at age *R*.0+ were found. Such males return to rivers after some months of marine life and do not overwinter in the sea. Some jacks previously spawned as parr, while others did not. All jacks and normal-sized sea-run males die after spawning. Thus, male masu salmon mature as one of four life history forms: (1) male parr, (2) jacks that matured previously as parr, (3) jacks that did not mature previously as parr, and (4) ordinary sea-run males. While mature male parr and sea-run males are ordinary life history forms, both forms of jack are rare.

À South Primor'e (Russie), on trouve des tacons mâles matures de saumon japonais (*Oncorhynchus masou*) dont l'âge est compris entre 0+ et 3+ (9 à 22 cm). Après une première maturation, quelques fatons mâles meurent, tandis que d'autres survivent et atteignent la maturité sexuelle l'année suivante. Les mâles immatures deviennent des smolts après un ou deux hivers passés dans les rivières et migrent en mer au cours du printemps jusqu'au début de l'été. Après avoir passé un hiver en mer, ils reviennent à l'état de mâles anadromes de taille normale (40 à 70 cm) à l'âge de *R*.1+. Outre des tacons mâles matures et des mâles anadromes de taille normale, on a observé la présence de jacks (28 à 33 cm) d'âge *R*.0+. Ces mâles reviennent dans les cours d'eau après quelques mois de vie en mer et ne passent pas l'hiver en mer. Certains jacks ont déjà frayé à l'état de tacon. Tous les jacks et les mâles anadromes de taille normale meurent après avoir frayé. Les saumons japonais mâles atteignent donc la maturité sexuelle à l'un des quatre stades biologiques suivants : 1) tacons mâles, 2) jacks qui ont déjà atteint la maturité à l'état de tacon, 3) jacks qui n'ont pas encore atteint la maturité à l'état de tacon et 4) mâles anadromes ordinaires. Les tacons mâles matures et les mâles anadromes sont des formes biologiques normales, pourtant les deux formes de jack sont rares.

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The majority of masu (or cherry) salmon (*Oncorhynchus masou*) (Brevoort) are sea-run fish. Usually, juvenile masu salmon spend 1 or 2 yr in rivers until their seaward migration (Machidori and Kato 1984; Tsygir 1988). During their freshwater life, some male parr mature at age 0+ to 2+. Mature male parr (or precocious, dwarf, neotenic, resident, residual males) of masu salmon occur throughout the species' range (Oshima 1934; Semko 1956; Krykhtin 1962; Tanaka 1965; Utoh 1976, 1977; Ivankov et al. 1977; Semenchenko 1989). Females rarely mature at the parr stage, and those that do are known only from southern regions (Behnke et al. 1962; Ivankov et al. 1981; Kimura 1989).

That male masu salmon mature at the parr stage is well known, but there are few data on their life after spawning. Some authors (Oshima 1934; Ikuta et al. 1987) reported that 0+ mature male parr survive after discharging their sperm and ripen again the next fall. Krykhtin (1962) stated that the fate of mature male parr was not clear. Despite an intensive search, he found only one dead postspawning mature male parr. Therefore, he suggested that while some male parr died after spawning, others migrated to sea and became normal sea-run males. Tanaka (1965, p. 98) reported that in experiments, masu salmon matured at the parr stage two or more times.

Ivankov et al. (1977) revealed that in testicles of post-spawning male parr, spermatozoids are resorbed and gonads filled anew by spermatogonia. As a result, at the parr stage, males can mature the following year after their first maturation. These authors found one dead postspawning male parr at age 2+. Therefore, they suggested that some male parr died after their second maturity, but a few might also mature three times.

Aida et al. (1984) suggested that maturation at the parr stage prohibited smoltification, but some mature male parr became smolts in experiments conducted by Sato et al. (1985). Other researchers (Bushuev et al. 1988; Bushuev 1990) also have not excluded the possibility that mature male parr of masu salmon can adapt to seawater.

Masu salmon usually spend only one winter in the ocean (Machidori and Kato 1984; Tsygir 1988), and sea-run males

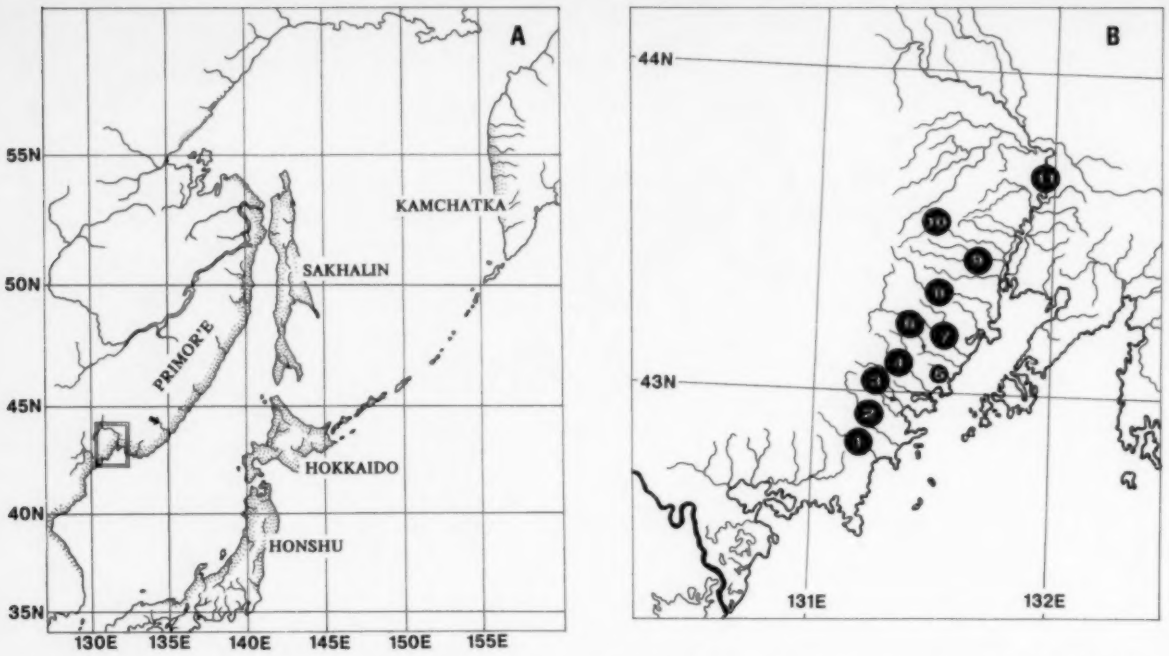

FIG. 1. (A) Region of distribution of sea-run masu salmon (stippled). Arrow indicates the Avvakumovka River. (B) South Primor'e (inset, Fig. 1A) where field research was conducted. Rivers: 1, Ryazanovka; 2, Poima; 3, Taksani; 4, Narva, 5, Sukhaya; 6, Kedrovka; 7, Barabashevka; 8, Amba; 9, Elduga; 10, Sanduga; 11, Razdol'naya.

of masu return to rivers at age $R.1+$[1]. In the rivers of Primor'e, their fork length varies from 40 to 70 cm (Ivankov et al. 1984; Semenchenko 1989; this study). Recently, two small sea-run males with fork lengths near 30 cm have been discovered in the rivers of South Primor'e (Erokhin et al. 1983; Semenchenko 1985).

Erokhin et al. (1983) reported the capture of a small mature anadromous male (27 cm fork length) near the mouth of the Narva River. Semenchenko (1985) described an age 3.0+ male from the Kedrovka River. Ivankov and Ogorodnikov (1991) mentioned capture of masu salmon of age 1.0+. There are no reports of maturing anadromous masu salmon from Japanese and Korean rivers which did not winter in the sea; in the latest review of the life history of masu salmon (Kato 1991), nothing was said about the existence of such life forms.

In this paper, we present new data on mature male parr and returning sea-run male masu salmon from the region of South Primor'e.

Materials and Methods

Usually, adults for biological analysis were sampled in South Primor'e by gill nets with stretch mesh ≥100 mm. Therefore, anadromous fishes with body lengths nearer 30 cm might be caught only accidentally. Other fishing gear could not be productively used because masu adults migrate into rivers immediately after typhoons when water levels in the rivers are high. At these times, use of seine nets or traps is impossible. When water levels are low, few adults migrate.

Masu salmon adults were sampled in the mouth of the Narva River on one day and one night within 5–10 d from July to September using gill nets 50–100 m long with a stretch mesh of 100–140 mm. During 1987–91, data on 50–200 adults from the mouth of the Narva River were collected each year. Occasionally, adults were sampled by the same gill nets in three other rivers: Ryazanovka, Poima, and Razdol'naya (Fig. 1). In these rivers, 20–50 adults were sampled each year. In attempts to catch small anadromous fishes in 1988–89, we occasionally used three-panel gill nets, the middle panel having a stretch mesh of 72 mm, but we succeeded in catching only normal-sized adults.

Spawning grounds were searched for normal-sized sea-run fish, small anadromous males, and dead postspawning male parr during 1987–91 in the Rivers Ryazanovka, Poima, Narva, Kedrovka, and Barabashevka and in 1987–88 in the Sukhaya River. We also asked fishermen to show us any small individuals of sea-run masu salmon they caught and to inform us of anyone capturing small sea-run fish.

During 1988–91, juveniles were sampled in seven rivers of South Primor'e using a seine net 11 m long with a 14-mm stretch mesh. The Rivers Ryazanovka, Poima, Narva, Barabashevka, Amba, Elduga, and Sanduga (Fig. 1) were sampled from April to October. Samples of smolts were collected in April and May once or twice each year. For collection of one sample of smolts in the lower parts of each river, several casts were made. Common places of

[1]In the age designation, the digit before the decimal point signifies the number of winters in the river and the digit after the point the number of winters at sea. When the number of winters in the river is of no significance, in this paper the letter "*R*" is used. In the case of masu salmon the "*R*' may range from 1 to 3.

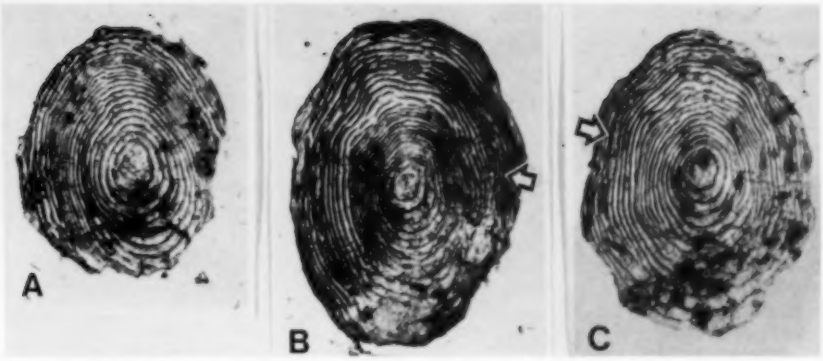

FIG. 2. Scales of postspawning dead male parr of masu salmon. (A) Age 1+, strong resorption of scale. (B) Age 1+SM+, resorption of scale is weak. Spawning mark (arrow), formed at the second year of life also, is weak and characterized only by erosion along the side of the scale. (C) Age 1+SM+. Spawning mark (arrow) characterized by erosion of anterior and posterior parts.

smolt habitation (pools and riffles) were selected for fishing. The lowest point of sampling was the mouth of the Narva River, where there was an observation station of the Pacific Research Institute of Fishery and Oceanography. At this location, a seine net 50 m long with a stretch mesh of 20 mm was used. The sampling was stopped when 50–100 fish were caught. We collected 12 samples of smolts in six rivers in 1988, 14 samples in seven rivers in 1989, 10 samples in seven rivers in 1990, and nine samples in seven rivers in 1991.

Smolts were classified as "pre-smolt", "mid-smolt", and "post-smolt" according to the stages described by Kubo (1974, 1980). Sexual maturity was determined visually according to the six-stage scale of maturity (Pravdin 1966; Nikolskiy 1974). Samples were fixed in 10% formalin solution; each fish and one gonad of each male were later weighed and the gonadosomatic index (GSI) calculated as

$$((\text{gonad weight} \times 2)/\text{body weight}) \times 100\%.$$

Salmon that have matured twice can sometimes be identified from their scales (Oshima 1934; Zamakhaev 1948; Bagliniere and Maisse 1985; Davis and Light 1985). We therefore investigated scales from 6000 juvenile masu, 700 mature male parr, and more than 1000 adults. Scales were sampled from the area between the dorsal and adipose fins (Clutter and Whitesel 1956).

We found that there were spawning marks (SM) on the scales of some mature male parr of masu salmon. Spawning checks were identified from resorption on circuli and erosion on the scale surface. Spawning checks on scales of masu salmon are characterized by resorption of circuli mostly in the posterior part of the scale. This resorption is less noticeable or nonexistent on the anterior part of the scale (Fig. 2). Such checks were found on the scales of male parr, but never on scales of juvenile masu and normal-sized adults. Therefore, we believe that maturation was the reason for the formation of such checks.

We assume that the mechanism of formation of the spawning mark is the same as in other fish and may be described as follows. At the time of spawning the body weight of male parr can significantly decrease. Their scales are resorbed, particularly along the posterior edge (Fig. 2A) located in the pocket of skin. Decrease in body weight and destruction of scales in adults are much more significant

Fig. 3. Scale of anadromous female, age 1.1+, fork length 520 mm, caught in the sea near the mouth of the Ryazanovka River in June. Arrow indicates ring of displacement, which is formed after the freshwater zone. This is not a spawning mark because dwarf females cannot mature as 0+ fish. This check occurred on a single scale sampled from an area under the dorsal fin (Pravdin 1966).

than in mature male parr because the latter may feed at the time of spawning, while adults do not (Krykhtin 1962; Volovik 1963; Ivankov et al. 1977; this study). Despite this, some postspawning male parr may remain in poor condition until the next spring (they differ from nonmaturing juveniles by their thin bodies).

Until the fish resume growth (usually in spring), the scales remain unchanged. With new growth, wide ridges form under resorbed circuli, and the spawning ring looks as though it were cut at the sides, destroying some circuli (Fig. 2B). It seems clear, therefore, that spawning marks can form only in fish whose body weight has decreased and whose scales

TABLE 1. Mature male parr of masu salmon that died after spawning; fish were collected in four rivers of South Primor'e.

No.	River[a]	Date of collection (yr.mo.d)	Fork length, mm	Body weight, g	Gonad weight, mg	Age, yr	Food[c]	Comments[d]
1	N	88.09.28	131	18.2	115	1+	0	W
2	N	88.09.28	191	62.7	—	2+SM+	0	
3	B	88.09.29	192[b]	54.0	—	1+SM+	0	
4	B	88.09.29	184[b]	57.0	—	1+	0	
5	B	88.09.29	162	41.0	1250	1+SM+	++	
6	B	88.09.29	167	46.0	660	1+SM+	++	
7	B	88.09.29	144[b]	26.5	440	1+	++	
8	P	88.11.11	122	11.5	138	1+		
9	N	89.09.27	125	—	—	1+	+	
10	N	89.09.27	153	39.0	400	1+SM+		
11	P	89.09.28	152	26.0	—	1+		
12	R	89.09.29	123[b]	—	—	1+		
13	R	89.09.29	172[b]	—	—	1+SM+		
14	B	89.10.06	245	—	—	2+		
15	B	89.10.06	158	—	—	2+		
16	B	89.10.06	126	26.5	610	1+	0	W
17	N	89.10.07	155	—	—	2+		
18	N	89.10.07	117	—	—	1+		
19	R	89.10.29	165	29.0	—	2+	0	FT
20	R	89.11.23	190	48.0	—	2+	0	W
21	R	89.11.23	165	—	—	2+	++	
22	B	91.09.19	120	18.5	1550	1+	++	W, FT
23	B	91.09.19	117	18.0	1070	1+	++	W, FT
24	N	91.09.23	225	84.0	—	2+		
25	N	91.09.23	167	51.5	2290	1+SM+	0	
26	N	91.09.23	125	16.4	—	1+	0	
27	P	91.09.24	123	20.0	1650	1+	0	
28	P	91.09.24	104	10.7	710	1+	0	
29	R	91.09.25	171	56.5	3340	1+SM+	0	W
30	R	91.09.25	152	35.8	980	1+	0	

[a]N, Narva; B, Barabashevka; P, Poima; R, Ryazanovka.
[b]Fork length (FL) calculated as FL = 0.212 + 1.071 × SL (standard length from mouth to posterior end of scale on caudal penduncle).
[c]0, empty stomach; +, small amount of food; ++, full stomach.
[d]W, wounds on body from adults' teeth; FT, testis full of sperm.

have eroded. However, there is no erosion (or erosion is insignificant) on the scales of some dead postspawning mature male parr (Fig. 2B and 2C).

So-called "rings of displacement" resemble spawning checks (Fig. 3). They may form as a result of scales turning in the pocket of skin (Zamakhaev 1948). Such rings are few on scales of any one fish and may occur on only one scale, while spawning marks occur on many. For this reason, we studied 10–20 scales from each fish to ensure we were looking at spawning checks.

Results and Discussion

Observations on the spawning grounds revealed that some mature parr as well as sea-run males of masu salmon died soon after spawning. Thirty dead postspawning male parr were found during the 1988–91 seasons (Table 1). There was a small amount of sperm in the testes of some fish. These males probably spawned in the season they were found, but others evidently had not yet spawned because their testes were full of sperm. Stomachs of some mature male parr were empty and had degenerated. These males had apparently not fed during the spawning season. There was some food (imago and larvas of aerial insects) in the stomachs of other males, indicating that they had fed before dying.

Some dead males had spawning marks on their scales formed in previous years (Fig. 2B and 2C). These fish therefore matured twice at a minimum: once in the collecting season and once the year before. Other dead male parr had no spawning marks on their scales (Fig. 2A). They probably died after their first maturation, but we cannot exclude the possibility that such fish died after their second maturation, the spawning marks having failed to form after their first maturation.

Dominance hierarchies occur among masu males during spawning as well as in other species of salmon. Anadromous males usually attack mature male parr, and some parr had wounds that they probably received from anadromous spawners. Wounds appeared as cuts across the body approximately 4–12 mm long and 1–2 mm wide (Fig. 4A) or as torn pits about 2–5 mm in diameter.

In 1988, we found four mature male parr in the stomachs of postspawning sea-run fish. Three were eaten by sea-run males and one by an anadromous female. In one case, we found two small masu salmon in the stomach of a postspawn-

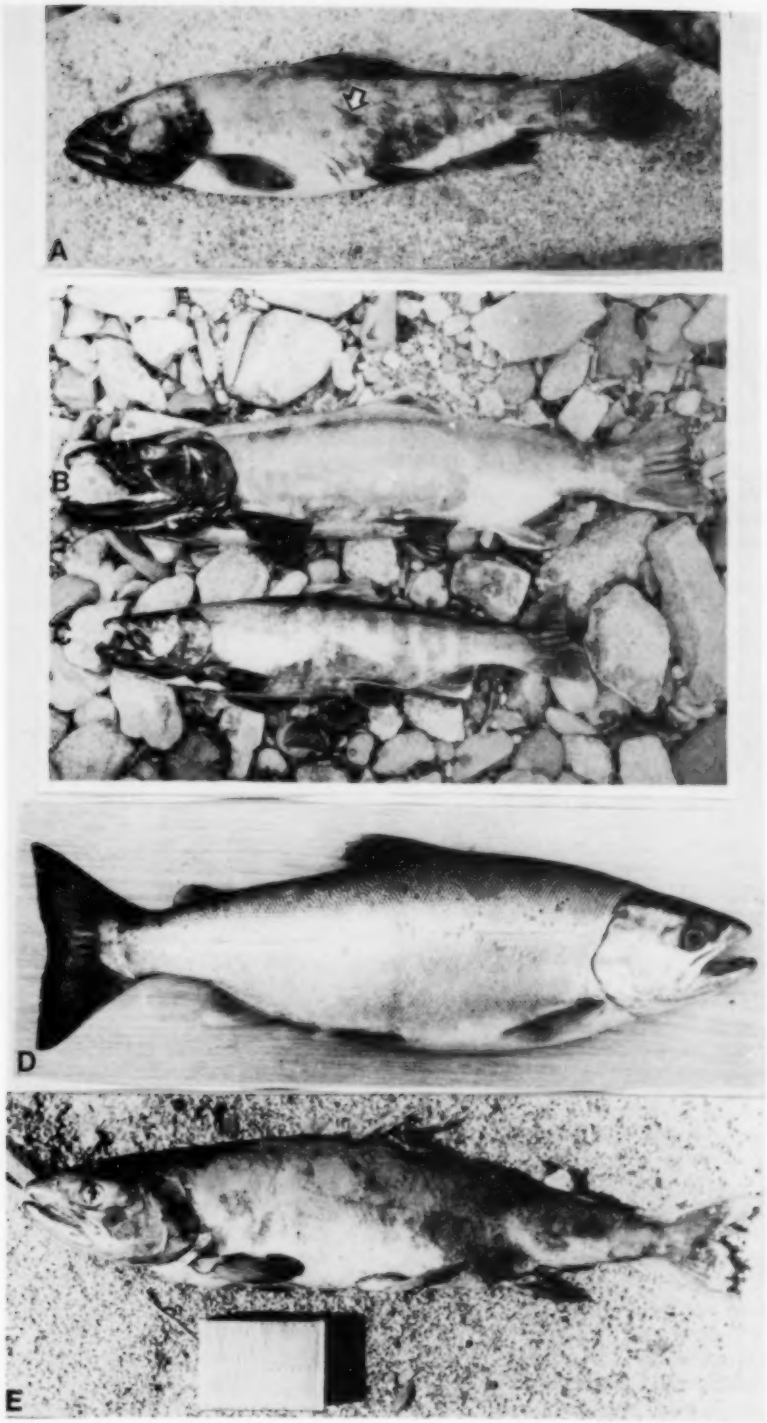

FIG. 4. Masu salmon males. (A) Dead mature male parr (No. 29, Table 1). Arrow indicates wounds from sea-run adults. (B) Sea-run male, age 2.1+, fork length 610 mm, collected in the Ryazanovka River as a dead fish. (C) Sea-run male, age 2.1+, fork length 440 mm, collected in the Ryazanovka River as a live spawning fish. (D) Silver jack, age 1.0+, collected in the mouth of the Narva River (No. 5, Table 3). (E) One of two jacks found dead in the spawning ground, former mature male parr (No. 8, Table 3).

TABLE 2. Details of recorded piscivory of postspawning masu salmon adults.

No.	River	Date (yr.mo.d)	Adults[a] Fork length, mm	Adults[a] Sex	FL (mm) of parr in stomachs[c]
1	Poima	89.09.28	565[b]	Male	138
2	Poima	89.09.28	601	Male	132
3	Ryazanovka	89.09.29	525	Male	110
					90
4	Ryazanovka	89.09.29	596[b]	Female	107

[a]All except No. 2 were dead.
[b]Fork length calculated as in Table 1.
[c]Four ingested parr were mature masu salmon males. A fifth and smallest (90 mm) from the stomach of No. 3 was also a masu salmon parr, but the sex was not distinguishable.

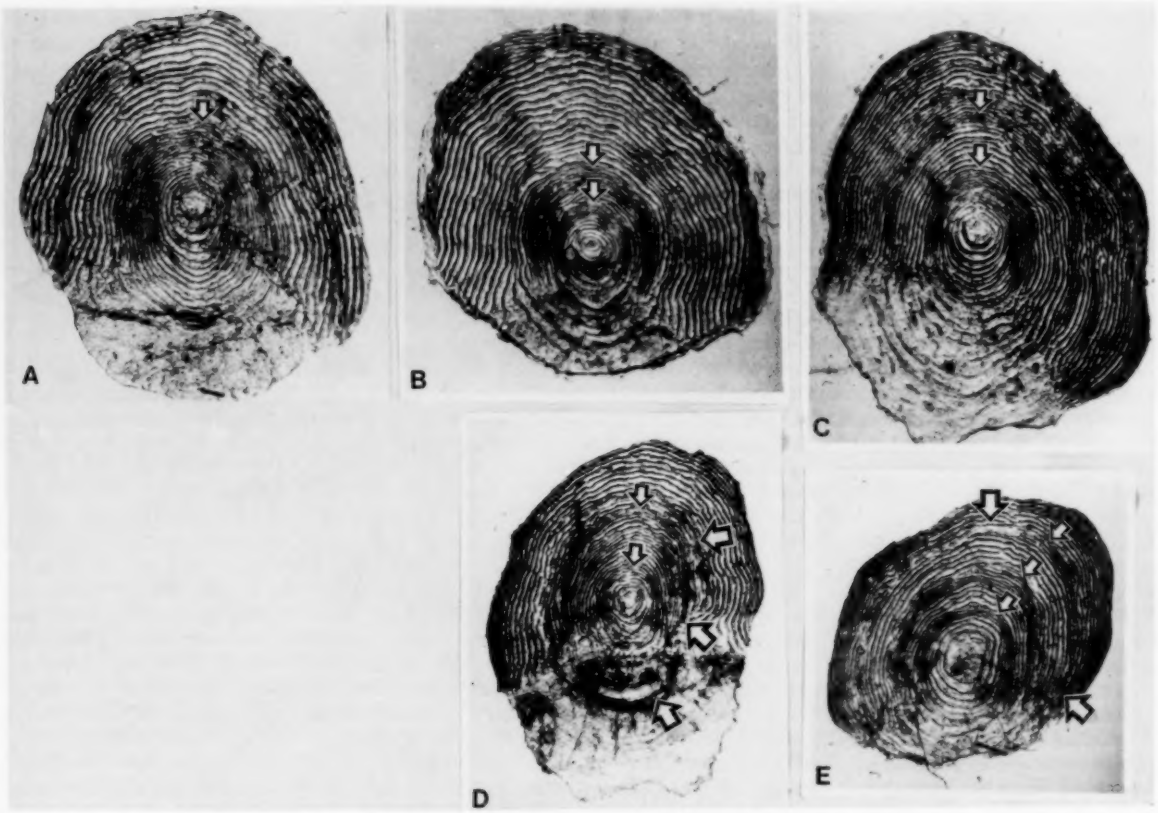

FIG. 5. Scales from (A–C) three of seven masu salmon jacks without spawning marks and from (D–E) two of two with spawning checks. (A) Age 1.0+ (No. 1, Table 3). Arrow indicates the end of the freshwater zone. (B) Scale from No. 9 (Table 3). (C) Scale from No. 3 (Table 3; Fig. 5D). (D) No. 7 (Table 3; Fig. 5E). (E). No. 6 (Table 3). Small arrows indicate freshwater annulus and large arrows indicate spawning marks, which occurred on many scales.

ing male (one was a mature male parr; the sex of the other was unrecognizable) (Table 2).

Many authors reported that mature male parr of masu salmon successfully continued to feed through the spawning season (Krykhtin 1962; Volovik 1963; Ivankov et al. 1977). However, we found that some dead male parr had degenerated digestive organs and empty stomachs (Table 1). Consequently, processes similar to those in sea-run adults occurred in some male parr and may have been the reason for their death.

Two fish had sperm in their testes and food in their stomachs (Nos. 22 and 23, Table 1). These fish had fed during the spawning season and did not suffer the same irreversible processes as did anadromous spawners. But those males had wounds on their bodies that may have been inflicted by adults' teeth and appeared to have died from the wounds.

TABLE 3. Masu salmon jacks from rivers of South Primor'e. Data and scales of fish No. 4 were contributed by the staff of Primorrybvod (Ussuriiskaya Observational Station); fish No. 6 was earlier described by Semenchenko (1985) but spawning marks on scales were not reported.

No.	River	Date of collection (yr.mo.d)	Fork length, mm	Body weight, g	Stage of maturity	Age, yr	Recovery location
1	Narva	85.10.04	306	210	6	1.0+	Mouth[b]
2	Narva	89.10.?	287	—	6	2.0+	Mouth[b]
3	Narva	91.09.05	278	362	4	1.0+	Mouth
4	Razdolnaya	72.08.11	315	385	3–4	2.0+	River
5	Barabashevka	87.10.03	325[a]	—	6	1.0+	Spawning ground
6	Kedrovka	80.09.15	295	—	5–6	2+SM.0+	Spawning ground
7	Kedrovka	89.10.06	290[a]	220	6	1+SM.0+	Spawning ground
8	Taksani	90.09.01	312	345	4	2.0+	Spawning ground
9	Poima	91.10.?	325	380	4–5	2.0+	River

[a]Fork length calculated as in Table 1.
[b]Fish were caught by seine net during the fishery for chum salmon.

Mature male parr of Atlantic salmon (*Salmo salar*) have been reported also to have died after injury from sea-run males (Hutchings and Myers 1987).

While many mature male parr appear to die in the wild mostly from poor condition or wounds, their survival in hatcheries is much better. For example, when juveniles and mature male parr were reared in hatchery tanks, no fish died during autumn and winter after maturing. All males (more than 200) survived and matured the following year. Consequently, survival of mature male parr in artificial conditions is much higher than in nature.

A high and constant mortality of mature male parr in rivers causes differences in sex ratios between juveniles and smolts. Usually the sex ratio among juveniles is nearly equal, while in smolts and anadromous adults, females always predominate (Machidori and Kato 1984; Okazaki 1989). Consequently, a significant proportion of males, probably mature male parr, die and never migrate to the ocean.

Mature male parr were found in all rivers studied. Usually, they have a dark or yellow body color. The age of maturity was 1+ and 2+, and a few were age 0+ and 3+. Fork length of mature male parr varied from 9 to 22 cm. Sometimes, fishes had traces of former spawning: scars on their bodies and/or spawning marks on their scales.

Besides normal sea-run males (with fork lengths 40–70 cm and age *R*.1+) (Fig. 4B and 4C) and mature male parr, small anadromous males were also found (Fig. 4D and 4E). Their fork lengths were about 30 cm. On the basis of scales (Fig. 5) and otoliths, these fish apparently spent only some months in the sea and did not overwinter there (Table 3). Since many masu, like coho salmon (*Oncorhynchus kisutch*), spend one winter in the sea, these males are analogous to coho salmon jacks, which did not overwinter in the ocean. We shall therefore also call small anadromous masu salmon males "jacks". Table 3 presents data on all collected jacks (nine individuals in total).

In South Primor'e, masu jacks were found in rivers of different size: in creeks about 15–20 km long (Taksani, Sukhaya, Kedrovka), in rivers 30–70 km long (Ryazanovka, Poima, Narva, Barabashevka), and in tributaries of big rivers (Razdol'naya) (Fig. 1). One jack was caught in the mouth of the Narva River by gill net (No. 3, Table 3) when migrating upstream together with normal-sized migrants. Another such case was mentioned by Erokhin et al. (1983). Four jacks (Nos. 3, 4, 8, and 9, Table 3) had silver-colored bodies (Fig. 4D). The jack from Poima River (No. 9, Table 3) was trapped in the downstream part of the river and had silver color, although with slightly pink bands, a characteristic of spawning color. Two jacks (Nos. 5 and 7, Table 3) were found dead and partially decomposed (Fig. 4E). Two jacks (Nos. 1 and 2, Table 3) were caught by seine net in the estuary of the Narva River as postspawning fish when the fishery for chum salmon (*Oncorhynchus keta*) was underway in October. Some small males, which were jacks, judging from their body length (about 30 cm), were seen on the spawning grounds, but we could not catch them.

Total percentage of masu jacks among all observed fish was very low in South Primor'e. We estimate that it was less than 0.5%. The percentage of jacks probably varies from year to year.

Seven masu salmon jacks had no spawning marks on their scales (Table 3; Fig. 5A–5C) and two fishes had spawning checks (Table 3; Fig. 5D and 5E). Both small anadromous males with spawning marks on their scales were from the Kedrovka River (Fig. 1). Spawning marks on jacks' scales have until now not been reported.

As previously mentioned, two dead jacks were found on the spawning grounds (Table 3; Fig. 4E). Two postspawning jacks were caught in the mouth of the Narva River near the sea, and one male had a smelt of about 10 cm in its throat (No. 1, Table 3). However, we never observed evidence of previous spawning at either the parr or jack stage in normal-sized sea-run adults. Therefore, we believe that all masu salmon jacks die after spawning like adults of the *R*.1+ age group.

Besides mature jacks, some male smolts were found that had sufficiently developed gonads to reach maturity later in the same year (Table 4; Fig. 6B). Usually in smolts the testes were thready or slightly thick (stage 2) (Fig. 6C). The GSI of ordinary male smolts varied from 0.008 to 0.105 (on average 0.036 ± 0.001). The testes of some fish appeared thick and, as we estimated, were at stage 2–3 or 3. The GSI of these fish varied from 0.062 to 0.537 (on average 0.214 ± 0.012).

Salmon males that have such large gonads in spring have been considered to have matured in the current season. Usually the criterion is that if the male gonad weight exceeds 0.1% of body weight in the beginning of the season, these

TABLE 4. Smoltified male masu salmon (presumed potential jacks).

No.	River[a]	Date (yr.mo.d)	Distance from sea[b]	Fork length, mm	Body weight, g	Stage of maturity	Gonad weight, mg	GSI, %	Age, yr	Stage of smolt[c]
1	N	87.06.04	20 m	127	20.9	3	105	0.502	2+	E
2	N	87.06.04	20 m	95	11.2	3	54	0.482	1	E
3	R	88.04.19	9 km	105	12.5	2–3	22	0.176	1+	E
4	R	88.04.19	9 km	119	24.1	3	60	0.249	1+	E
5	R	88.04.19	9 km	116	22.6	2–3	25	0.111	1+	M
6	P	88.05.20	6 km	103	12.4	3	—	—	1+	E
7	N	88.04.31	40 m	149	35.6	6–3[d]	114	0.320	2+	M
8	N	88.04.31	40 m	166	55.0	6–3[d]	134	0.244	1+SM+	M
9	N	88.04.31	40 m	165	52.2	6–3[d]	190	0.364	2+	M
10	N	88.04.31	40 m	137	30.2	2–3	40	0.132	2+	M
11	N	88.04.31	40 m	141	36.0	6–3[d]	113	0.314	2+	M
12	N	88.04.31	40 m	151	43.4	3	88	0.203	2+	M
13	N	88.04.31	40 m	130	28.9	3	27	0.093	1+	M
14	N	88.04.31	40 m	118	22.0	3	—	—	1+	M
15	N	88.05.20	40 m	135	27.9	3	56	0.201	2+	L
16	B	88.04.15	24 km	98	11.9	2–3	24	0.202	1+	E
17	B	88.05.20	14 km	92	9.7	2–3	30	0.309	1+	E
18	B	88.05.20	14 km	119	20.6	2–3	40	0.194	1+	M
19	B	88.05.20	14 km	110	17.9	2–3	50	0.279	1+	M
20	B	88.05.20	14 km	117	22.6	2–3	30	0.133	1+	E
21	B	88.05.20	14 km	113	18.1	2–3	36	0.199	1+	E
22	A	88.04.27	16 km	165	62.5	6–3[d]	—	—	1+SM+	M
23	A	88.05.20	16 km	100	13.0	2–3	—	—	1+	E
24	E	88.04.27	7 km	139	31.5	2–3	—	—	2+	E
25	R	89.04.27	6 km	118	20.4	3	84	0.412	2+	E
26	N	89.04.27	8 km	147	38.7	2–3	24	0.062	2+	L
27	N	89.04.27	8 km	166	58.3	3	150	0.257	2+	E
28	N	89.04.27	8 km	183	78.2	3	180	0.230	2+	E
29	N	89.05.12	8 km	101	13.8	2–3	—	—	1+	E
30	B	89.04.27	7 km	125	23.7	2–3	30	0.127	1+	E
31	B	89.04.27	7 km	140	38.1	3	50	0.131	2+	E
32	B	89.05.13	14 km	127	29.3	3	60	0.205	1+	E
33	R	90.04.24	5 km	114	18.3	2–3	—	—	1+	E
34	R	90.04.24	5 km	110	17.3	2–3	—	—	1+	M
35	R	90.04.24	5 km	110	17.0	2–3	—	—	1+	E
36	P	90.04.29	3 km	100	12.5	2–3	36	0.288	1+	E
37	P	90.05.15	3 km	135	29.8	2–3	20	0.067	1+	L
38	P	90.05.15	3 km	102	13.5	3	36	0.267	1+	E
39	P	90.05.15	3 km	106	14.0	2–3	24	0.171	2+	E
40	N	90.04.29	9 km	141	39.0	3	76	0.195	2+	E
41	N	90.05.15	8 km	105	14.4	2–3	24	0.167	1+	E
42	N	90.05.15	8 km	95	10.9	2–3	24	0.220	1+	E
43	N	90.05.15	8 km	101	13.2	2–3	18	0.136	1+	E
44	N	90.05.15	8 km	84	7.0	2–3	10	0.143	1+	E
45	B	90.04.18	22 km	110	17.7	2–3	40	0.226	1+	M
46	B	90.04.18	22 km	82	8.1	2–3	16	0.198	1+	E
47	B	90.04.18	22 km	130	33.5	3	—	—	1+	M
48	B	90.04.18	22 km	90	10.5	2–3	24	0.229	1+	M
49	B	90.04.18	22 km	85	8.8	2–3	24	0.273	1+	M
50	B	90.05.03	22 km	124	25.1	3	—	—	2+	E
51	B	90.05.03	22 km	144	43.2	3	176	0.407	1+	E
52	B	90.05.03	22 km	94	11.0	2–3	12	0.109	1+	E
53	B	90.05.03	22 km	102	14.0	2–3	24	0.171	1+	E
54	B	90.05.03	22 km	160	60.9	3–3	130	0.213	1+	E
55	B	90.05.03	22 km	135	38.1	2–3	40	0.105	1+	M
56	B	90.05.03	22 km	118	23.2	2–3	16	0.069	2+	M
57	B	90.05.03	22 km	151	50.1	2–3	48	0.096	2+	L
58	A	90.05.15	16 km	95	11.3	2–3	16	0.142	1+	E
59	S	90.05.15	16 km	102	14.6	2–3	40	0.274	1+	E
60	S	90.05.15	16 km	106	16.3	2–3	40	0.245	1+	E
61	S	90.05.15	16 km	96	12.2	2–3	—	—	1+	E
62	R	91.04.26	5 km	166	55.0	3	180	0.327	2+	E

TABLE 4. (*Concluded*)

No.	River[a]	Date (yr.mo.d)	Distance from sea[b]	Fork length, mm	Body weight, g	Stage of maturity	Gonad weight, mg	GSI, %	Age, yr	Stage of smolt[c]
63	R	91.04.26	5 km	140	32.5	3	124	0.382	2+	E
64	R	91.04.26	5 km	125	24.7	2–3	40	0.162	2+	E
65	P	91.04.26	3 km	177	69.0	3	240	0.348	2+	E
66	P	91.04.26	3 km	124	27.5	2–3	24	0.087	1+	M
67	P	91.04.26	3 km	143	37.8	3	90	0.238	2+	E
68	P	91.04.26	3 km	106	16.8	2–3	22	0.131	1+	E
69	N	91.04.26	8 km	124	23.6	3	50	0.212	1+	E
70	N	91.04.26	8 km	101	13.2	2–3	24	0.182	1+	E
71	A	91.04.25	16 km	162	53.6	3	—	—	2+	E
72	A	91.04.25	16 km	165	54.0	3	290	0.537	2+	E
73	E	91.05.21	7 km	91	9.6	2–3	24	0.250	1+	E
74	S	91.04.25	10 km	108	16.3	2–3	28	0.172	1+	E
75	S	91.04.25	10 km	110	15.0	2–3	36	0.240	1+	E

[a]N, Narva; R, Ryazanovka; P, Poima; B, Barabashevka; A, Amba; E, Elduga; S, Sanduga.
[b]Distance to the Razdolnaya River for the Elduga and Sanduga rivers.
[c]E, early stage, presmolt; M, midsmolt; L, late stage, postsmolt.
[d]Fish had characters of previous maturation.

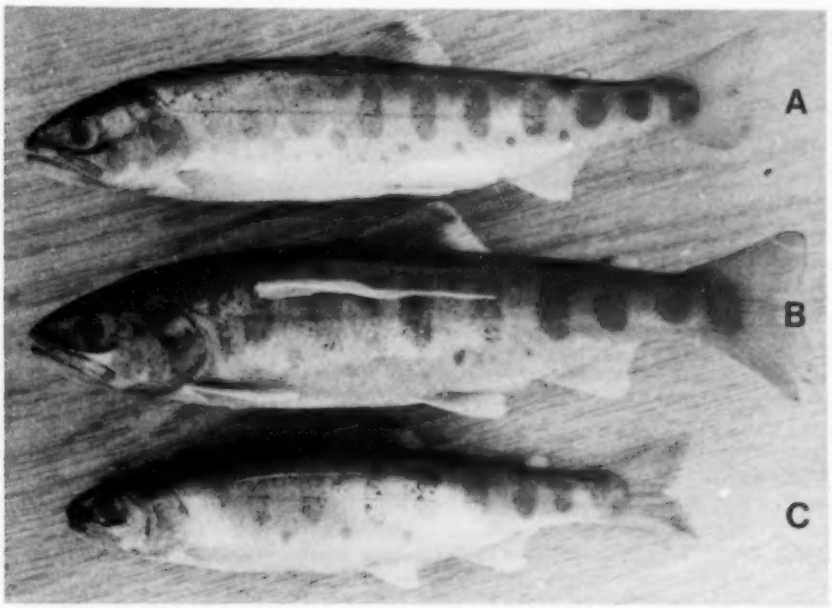

FIG. 6. Masu salmon smolts. (A) Female presmolt. Masu salmon females such as this >12 cm in April must enter the sea this season in South Primor'e. Compare the appearance of this seaward-migrating fish with that of potential jacks. (B) Male presmolt, gonad magurity 3, possible potential jack; upper part of dorsal fin slightly darkened (No. 65, Table 4). Exterior is similar to that of the female smolt in Fig. 6A. (C) Male midsmolt, gonad maturity stage 2. Upper part of the dorsal fin is completely darkened in contrast with presmolts in Fig. 6A and 6B. Fish fixed in 10% formalin; one gonad of males located on fish's body. Fish were caught in the Poima River, April 26, 1991, about 3 km up from the mouth of the river.

fish will mature that year (Murza 1983; Murza and Christophorov 1983; Sugiwaka and Kojima 1984; Kitamura 1991). Such male masu salmon smolts with developed testes must mature in the year of their seaward migration at age *R*.0+ and can therefore be referred to as "potential jacks".

The GSI of the majority of male smolts with gonads at stages 2–3 and 3 exceeded 0.1%, but the GSI of a few males did not (minimum GSI was 0.069) (Table 4). The GSI of a few smolts with gonads at stage 2 was greater than 0.1% (maximum was 0.105). The reason for this overlap is not clear. It may be a consequence of errors in visual determination of fish maturity or errors in calculation of GSI because only one gonad was weighed.

Male masu salmon that mature at the parr stage remain

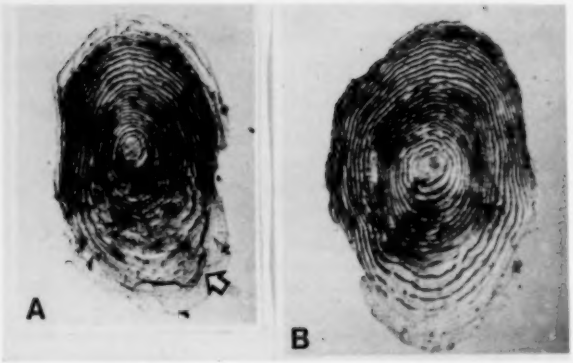

FIG. 7. Scales of postspawning masu salmon males (potential jacks). Appearance of these fish indicated that they matured the previous year. They were caught in the mouth of the Narva River April 28, 1988. (A) No. 6 (Table 4). (B) No. 7 (Table 4).

in the river and mature there a second time (Utoh 1976). However, we found a few male smolts that appeared to have matured the previous year. The changes in the form of head and bones that occur at spawning, and the darkening of some parts of the body seen in mature male parr, still remained. The scales of a few fish revealed weak spawning marks (Table 4; Fig. 7A). Gonads of these males were thicker than ordinary male smolts; the GSI exceeded 0.2% (Table 4).

Capture of these fish in the river mouth suggests that they were migrating to sea. This fact corresponds with the discovery of spawning marks on scales of some jacks and confirms that some postspawning male parr can migrate to sea and become jacks. A few male smolts that spawned the previous year (they showed spawning changes to heads and bones and darkening of some parts of the body seen in mature male parr) had no spawning marks on their scales (Table 4; Fig. 7B). Therefore, some jacks without spawning marks (this study) may nevertheless have spawned before as parr.

Kubo (1974, 1980) divided masu salmon smolts into three stages: (1) presmolts, the early stage when the tip of the dorsal fin is slightly pigmented and parr marks appear through light silvering, (2) midsmolts, when pigmentation of the dorsal fin margin is rarely complete, and parr marks are less distinct, and (3) postsmolts, the completely smoltified stage in which parr marks are masked by guanine, and pigmentation of the dorsal fin margin is complete. Based on these criteria, male smolts with developed gonads that we collected usually were classified as presmolts or midsmolts (Fig. 6; Table 4). In a few cases, these males were estimated to be postsmolts (Table 4). According to Kubo (1974, 1980), some fish (so-called "pseudo-smolts") have external characters of smolts, but they remain in rivers and do not descend to the sea. Pseudo-smolts die within 2 d in seawater (Kubo 1980). The differentiation between pseudo-smolts and fish in early stages of smoltification is difficult, and the main distinctive character is that the pseudo-smolt's body is somewhat deeper than in true smolts.

Because the body of male smolts with developed testes is deeper than that of immature smolts, they resemble pseudo-smolts. Some potential jacks were caught in the mouth of the Narva River (about 20–40 m from sea) (Table 4). These fish may have been about to enter the sea. At the same time, many males estimated to be presmolts or midsmolts, with gonads in stage 2–3 or 3, were sampled far from the rivers' mouths (Table 4). Therefore, we cannot reject the possibility that fish (estimated as early- and midsmolts) could remain in rivers and revert to mature male parr. Nevertheless, the existence of jacks proves that some males with developed testes migrate to sea in spring and after some months return to rivers.

TABLE 5. Percentage of potential jacks in samples of smolts from all rivers (sample size in parentheses).

Year	Calculated from all smolts	Calculated from male smolts
1988	0.037 (600)	0.110 (201)
1989	0.012 (684)	0.035 (228)
1990	0.047 (616)	0.117 (247)
1991	0.031 (448)	0.081 (174)
Total	0.031 (2348)	0.086 (850)

The percentage of all male smolts with well-developed testes (potential jacks) was very low, as was the rate of jacks among normal anadromous adults. The percentage of potential jacks in all samples of smolts, collected in seven rivers of South Primor'e, varied in different years from 0.012 to 0.047%, or from 0.035 to 0.117% (if calculated only from males) (Table 5).

These results indicate that there are various life history forms of male masu salmon that can be found in the same population, as follows.

(1) Mature male parr (or precocious, dwarf, neotenic, resident, or residual males). These males mature in rivers at the parr stage and do not migrate to the sea. Some of the parr die after their first maturation and others after the second. A few males may mature at the parr stage three times.

(2) Jacks that matured earlier as parr. Males of this type mature in rivers at the parr stage, smoltify, and migrate next spring to the ocean, where they remain for several months, and then return to rivers to spawn. They die after maturation as jacks. These males may be considered intermediate between mature parr and sea-run males.

(3) Jacks that did not mature before smoltification. They live usually 1 or 2 yr in rivers and migrate to sea with developing gonads that mature in the year of seaward migration. They do not overwinter in the sea, and die after first maturation.

(4) Sea-run males are fish that live usually 1 or 2 yr in rivers and never mature there, migrate to sea as ordinary smolts, and mature usually the year after their seaward migration and die after first spawning.

Jacks probably occur only in southern areas, where there is sufficient time for maturation between seaward migration of smolts and return of adults. For example, the major part of the smolt run in South Primor'e takes place in May, and the adults return in August–September. In rivers of North Primor'e, Sakhalin, and West Kamchatka, seaward migration of smolts takes place usually in June. Return of adults occurs also in this month. Therefore, anadromous juveniles from northern regions have insufficient time to mature in the season of entrance to the ocean.

As is known, masu salmon at age *R*.0+ usually leave the

Japan Sea to enter the Okhotsk Sea in summer (Machidori and Kato 1984). The existence of jacks suggests that some fish from Primor'e rivers do not leave the Japan Sea, remaining, evidently, not far from their natal rivers.

Our data on jacks of masu salmon were collected in rivers discharging into the Bay of Peter the Great. However, masu salmon jacks are distributed more widely in South Primor'e. Fishermen report that small anadromous male masu salmon are caught in rivers as far north as the Avvakumovka River (arrow, Fig. 1A), but they are also very scarce there.

The existence of small anadromous males 30–33 cm in fork length has been reported for some rivers in the south of Sakhalin Island (Fig. 1A) (Ivankov et al. 1984; Makeev et al. 1990). However, Sakhalin masu salmon usually are of small size despite about 1 yr of marine life. Average fork length of males from two rivers in the south of Sakhalin Island (Fig. 1A) was only 37–41 cm (Ivankov et al. 1984). Therefore, the 30- to 33-cm males were probably not jacks, but rather age *R*.1+ salmon.

Residual spermatozoids in testicles of surviving postspawning male parr are resorbed and the testicles filled anew in autumn with spermatogonia (Ivankov et al. 1977). These parr return to the immature state in winter if they survive (Ikuta et al. 1987; this study). However, the GSI of all male smolts found with evidence of previous maturation exceeded 0.2% (Table 4). As we mentioned earlier, male salmon that have such large gonads in spring are considered to have matured in the current season. Therefore, seaward-migrating postspawning male parr must mature in the year of their seaward migration at age *R*.0+ and do not become normal sea-run males at age *R*.1+. Thus, maturation of males at the parr stage apparently prohibits their later return as adults of large size. Moreover, even transformation of formerly mature male parr into sea-run jacks is rare in masu salmon.

Transformation of mature male parr into sea-run males has been described for Atlantic salmon (Mitans 1973; Leizerovitch and Melnikova 1979; Bagliniere and Maisse 1985). For masu salmon, however, this is a new observation. Moreover, it is new for the genus *Oncorhynchus*.

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PERSPECTIVES

Long-term Experiments on the Stability of Two Fish Populations in Previously Unexploited Arctic Lakes

Lionel Johnson[1]

Department of Fisheries and Oceans, Freshwater Institute, 501 University Crescent, Winnipeg, MB R3T 2N6, Canada

Johnson, L. 1994. Long-term experiments on the stability of two fish populations in previously unexploited arctic lakes. Can. J. Fish. Aquat. Sci. 51: 209–225.

Previous research indicated that fish populations in arctic lakes maintain a constant size distribution and abundance in the face of the environmental variability experienced over their recent history. Such stability was tested over 15 seasons in Little Nauyuk and Gavia lakes (Northwest Territories) which contained previously undisturbed populations of Arctic char (*Salvelinus alpinus*). Initially, the length–frequency distribution of Arctic char in Little Nauyuk Lake was bell shaped, and in Gavia Lake, it could be described by a negative logarithmic expression. Initial sampling of Gavia Lake removed the largest fish, allowing a well-defined mode to develop (cf. Little Nauyuk Lake). In both lakes the modal value remained constant throughout the exploitation phase. When fishing ceased the populations returned to their original state without evident oscillation. The stable state of the dominant population is considered to be one of "least dissipation". It is hypothesized that ecosystem structure depends on countervailing forces, one tending to decelerate energy flow through the ecosystem and the second tending to accelerate it. For ecosystems to exist, the tendency to decelerate energy flow must dominate system behaviour over ecological time. An ecosystem is regarded as a hemeorhetic system, *stability seeking* through the stabilization of energy flows.

Des recherches antérieures ont montré que dans les lacs arctiques, la répartition selon la taille et l'abondance de populations de poissons sont constantes en dépit de la variabilité environnementale constatée au cours des dernières années. Une telle stabilité a été examinée sur une période de 15 saisons dans les lacs Little Nauyuk et Gavia (Territoires du Nord-Ouest) qui autrefois abritaient des populations vierges d'omble chevalier (*Salvelinus alpinus*). Initialement, la distribution en fonction de la longueur et de la fréquence de l'omble chevalier dans le lac Little Nauyuk était en forme de cloche et dans le lac Gavia, elle pouvait être décrite par une expression logarithmique négative. Lors de l'échantillonnage initial dans le lac Gavia, on a prélevé le plus grand poisson, ce qui a permis le développement d'un mode bien défini (voir lac Little Nauyuk). Dans les deux lacs, la valeur modale était constante pendant toute la phase d'exploitation. Lorsque la pêche a cessé, les populations sont revenues à leur état original sans oscillation évidente. L'état d'équilibre de la population dominante est considéré comme un état de « moindre dissipation ». On a émis l'hypothèse selon laquelle la structure de l'écosystème dépend de forces compensatrices, une tendant à ralentir le transfert d'énergie dans l'écosystème, la deuxième tendant à l'accélérer. Pour que les écosystèmes existent, la tendance à ralentir le transfert d'énergie doit dominer le comportement du système au cours du temps écologique. Un écosystème est considéré comme un système homéorthétique, c'est-à-dire tendant vers la stabilité, par le biais de la stabilisation des transferts d'énergie.

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Stability is the capacity of a system to return to its initial state following perturbation. Some ecologists see stability as a basic property of species populations and ecosystems; others deny its existence. My intention in this paper is to approach this conflict by examining the effect of controlled exploitation on previously stable Arctic char[2] (*Salvelinus alpinus*) populations in two arctic lakes.

The concept that the living world is maintained in balance by internal forces stretches back to the fifth century B.C., when Herodotus first formulated the notion which eventually came to be known as the "balance of nature". For many years, this remained accepted dogma. Writers such as Linnaeus (1749) emphasized the preservation of harmony and stability in biological communities, but, in the latter part of the eighteenth and early nineteenth centuries, evolutionary notions, incompatible with stability, were in the air (Egerton 1973). If stability were a property of ecological systems, then it was, at best, of a temporary nature.

The concept of balance was first seriously questioned by

[1]Present address: 10201 Wildflower Place, Sidney, BC V8L 3R3, Canada.

[2]The author prefers "charr" rather than the American Fisheries Society spelling used as the editorial standard in this journal.

Wallace. Wallace wrote (although this was later found as an entry in one of his notebooks and not published until 1966) (McKinney 1966, quoted by Egerton 1973)

> Some species exclude all others in particular tracts. Where is the balance?....To human apprehension there is no balance but a struggle in which one often exterminates another

More supportive of the concept of the balance of nature was Stephen A. Forbes' view of "The lake as a microcosm" (Forbes 1887, p. 549):

> For every defensive device with which she [nature] has armed an animal, she has invented a still more effective apparatus of destruction and bestowed it upon some foe, thus striving with unending pertinacity to outwit herself; and yet life does not perish in the lake, nor even oscillate to any considerable degree, but on the contrary the little community secluded here is as prosperous as if the state were one of profound and perpetual peace. Although every species has to fight its way inch by inch from the egg to maturity, yet no species is exterminated but each is maintained at a regular average number which we shall find good reason to believe is the greatest for which there is, year after year, a sufficient supply of food.

In plant ecology, similar ideas were developed by Clements (1905, 1916) into the concept of the supraorganism, in which the various species functioned in concert to provide stability (continuity) to the whole. These views were strongly challenged by Gleason (1917, 1939) who developed the individualistic approach to ecology. These individualistic ideas were supported by many ecologists of considerable influence and have gained wide acceptance. Elton (1930), for example, stated

> The balance of nature does not exist, and perhaps never has existed. The numbers of wild animals are constantly varying to a greater or less extent, and the variations are usually irregular in period and always irregular in amplitude. [Owing to interactions between species behaving similarly] the resultant confusion is remarkable.

The side of population stability and the balance of nature was taken by Nicholson (1933) and Slobodkin (Slobodkin 1964; Slobodkin et al. 1967), against those such as Andrewartha and Birch (1954) and Erlich and Birch (1967) who opposed the notion.

Dunbar (1960), discussing the stability of arctic marine ecosystems, recognized the inherent fluctuations of organisms in the marine environment, but nevertheless concluded

> The case may be made here, then, is that the stable non-oscillating system is the "ideal" and the product of a long process of evolution: and that the oscillating systems of regions affected by the present glacial climate of the world are in process of evolution towards better adjustment.

Even the participants in the well-known symposium on diversity and stability in ecological systems (Woodwell and Smith 1969) could not reach a definite conclusion on either the existence, nature, or magnitude of the forces inducing stability.

At the present time, the prevailing view seems to be that there is little or no stability in populations that would support a "balance of nature" concept, although Pimm (1984) concluded that

> nearly all natural populations are characterized by patterns of change that keep their numbers within bounds... only a minority of populations fluctuate so widely that an equilibrium is not obvious.

Therefore, it appears necessary to postulate that ecosystems exhibit at least a "temporary" stability, whether it be over long periods of geological time as indicated in the theory of punctuated equilibrium (Gould and Eldredge 1977) or over shorter periods of "successional" or "ecological" time.

After an extensive survey of the literature, Connell and Sousa (1983) could stated:

> There is, to our knowledge, no evidence to show that following a disturbance any community has adjusted back to an original species configuration which then resisted change beyond one complete turnover....In our opinion, the evidence gathered about numbers of animals and plants over the past 50 yr upholds Elton's description. If a balance of nature exists, it has proven exceedingly difficult to demonstrate.

And they provide a list of 49 long-term observations in which

> there is no clear demarcation between assemblages that may exist in an equilibrium state and those that do not. Only a few examples of what might be called stable limit cycles were found. There was no evidence of multiple stable states in unexploited natural populations or communities.

Much effort has been devoted to attempting to define stability in model ecosystems (May 1973), but none appear to support field observations except in a very limited way.

In effect (Egerton 1973),

> ...there was no science built, as Linnaeus would have it, around the balance of nature.

What is lacking is an adequate theoretical base against which notions of stability can be tested.

Stability

Pimm (1991), in his extensive work examining the balance of nature, could extract no overall generalities; for every example showing a specific trend, there is a counter example refuting the previous position. Confounding the issue is the fact that the term stability has been used to imply several different characteristics of species populations and ecosystems. Pimm identified five different usages of the term: (i) stability in the mathematical sense: a system is stable, if and only if, the variables all return to the equilibrium conditions after displacement from them; (ii) resilience: the rate at which a system returns to the equilibrium position from which it was displaced; (iii) persistence: the length of time a variable lasts before it is changed to a new value; (iv) resistance: the capacity to withstand a permanent change in a variable; and (v) variability: the degree to which a variable changes over time.

Inertia, constancy, conservatism, and endurance have also been used to express one or other of the many different aspects of stability (Connell and Sousa 1983). According to these authors:

> For a system to be considered stable there must exist one or more equilibrium points or limit cycles, (1) at which the system remains when faced with a disturb-

> ing factor or, (2) to which it returns if perturbed by a force. (Theoretically a system could have unstable equilibrium states which satisfy 1 but not 2: we will not consider this possibility further.) This concept requires two things a) the existence of stable equilibrium states which for the remainder of this paper [i.e., Connell and Sousa's] refer either to stable points or stable limit cycles; and (b) the existence of forces that may be capable of perturbing the system so that it is no longer at equilibrium. [A stable equilibrium they define as...] a particular state of a characteristic, e.g., population density, at which a population will remain, or if moved away from it, to which the population will return.

Hurd et al. (1971) developed a definition of stability based on thermodynamic considerations:

> Stability is the ability of a system to maintain or return to its ground state after an external perturbation. The *degree* of stability is characterized by (i) the amplitude of the deflection from the ground state, (ii) the rapidity of the response to perturbation, and (iii) the rate at which any deflection is damped.

An external perturbation is defined as one which leaves no trace in the environment when discontinued. Fishing for a set period of time, or an exceptionally severe winter, is an external perturbation, but the introduction of new species, a permanent environmental change (such as the introduction of nutrients), or the continuous imposition of what would otherwise be an external perturbation (e.g., continual fishing) is not and will tend to deform the system. A stable ecosystem demands a damping mechanism through which systems achieve a balance or equilibrium state.

In addition to the above criteria characterizing stability, a stable or equilibrium state should be capable of being characterized in general physical terms, comparable with "maximum entropy" in an isolated system (thermodynamic equilibrium) or "minimum potential energy" in a mechanical device. Any biological equilibrium that may be identified is a dynamic equilibrium (ergodynamic equilibrium, i.e., equilibrium maintained by work done), far from thermodynamic equilibrium (Johnson 1994).

If progress is to be made, the conditions in which ecosystem stability can be expected need to be defined. Ecological stability can be expected to occur only if, (i) the ecosystem forms a "closed" system exchanging only energy with the external world, (ii) the species complement remains constant, and (iii) the environmental variables fluctuate around mean values. Without a degree of isolation and constancy in energy input, a system may be expected to fluctuate. The degree of fluctuation will depend on the internal damping capacity of the system. As closed conditions exist in the real world only at the level of the whole biosphere and environments fluctuate, no local ecosystem can be expected to be stable in any absolute sense because of changing energy values. The nearest approach to the necessary conditions can be found in an autonomous ecosystem in which the exchange of biological material with the external world is minimal, and at the same time one that is not subjected to destructively large environmental fluctuations. The important question, then, is what are the forces which prevent real ecosystems from fluctuating to destruction when the boundary constraints are relatively low? Or as Pimm (1984) asked, "What is it that keeps most systems within bounds?"

Arctic Lake Ecosystems

According to Platt (1964), the study of complex systems should start with the simplest one available which contains all the parameters of interest. Barbour and Brown (1974) have shown that fish species richness in freshwater lakes declines with increasing latitude, although, in addition, the area of a lake was found to be highly significant. Given this decline in fish species richness with latitude, the logical place to begin a study of complex freshwater ecosystems is a small arctic lake. Arctic lake ecosystems are amongst the simplest known and are almost completely self-contained; they range in size from a few hectares to thousands of square kilometres. In addition, many have remained completely undisturbed by human activity since their formation in the closing stages of the Pleistocene. Long-term studies have shown that these lakes contain stable ecosystems. This conclusion is based on the observed structure of the dominant fish populations and the effect of perturbation on them (Johnson 1972, 1976, 1983). Such stability is relative and dependent on the constancy of the environmental driving mechanisms.

Drainage systems in the Arctic are, in general, poorly developed, and in many cases the lakes are isolated from connecting waterbodies by falls impassable to migrating fish. Only close to the coastline do migratory fish stocks exist. Although arctic lakes have few fish species, fish density is high and stocks are largely free from predators (Johnson 1972, 1976). The most northerly lakes (as well as many smaller lakes at somewhat lower latitudes) contain but a single species of fish, Arctic char (*Salvelinus alpinus*) (Johnson 1980, 1983; Parker and Johnson 1991). Comparable results have been obtained from lakes containing the single fish species Arctic char in Greenland (Sparholt 1985; Riget et al. 1986). Single species populations in such lakes express in isolation their inherent behaviour patterns, free from interaction with species at a similar or higher trophic level.

Investigations on northern lakes indicated that the dominant fish populations, whether lake trout (*Salvelinus namaycush*), lake whitefish (*Coregonus clupeaformis*), or Arctic char were composed of abundant, large individuals (mean length ≈450–600 mm). Samples exhibited bell-shaped length– and age–frequency distributions in which the modal length class was occupied by fish of considerable, but highly variable age (mean age ≈10–15 yr), although the modal size of populations in different lakes varied considerably. There was an apparent dearth of juvenile and intermediate-sized fish. These populations appeared to be stable in that (i) their age and size structure indicated little change over their recent history, (ii) a large number of lakes examined over a wide geographical range showed identical structure, (iii) similar structure was exhibited by the dominant species whether lake whitefish, lake trout, or Arctic char, (iv) observations on the same lake after an interval of many years showed little change (Johnson 1976, 1983, 1994, and (v) the Arctic char population in Keyhole Lake, Victoria Island, was severely perturbed between 1962 and 1967 (Hunter 1970); by 1975, it had returned to its original configuration, and this was maintained until 1985 (Johnson 1983; Vanriel 1989).

Stable arctic lake fish populations seemed to be at variance with the accepted model of the structure of a fish population

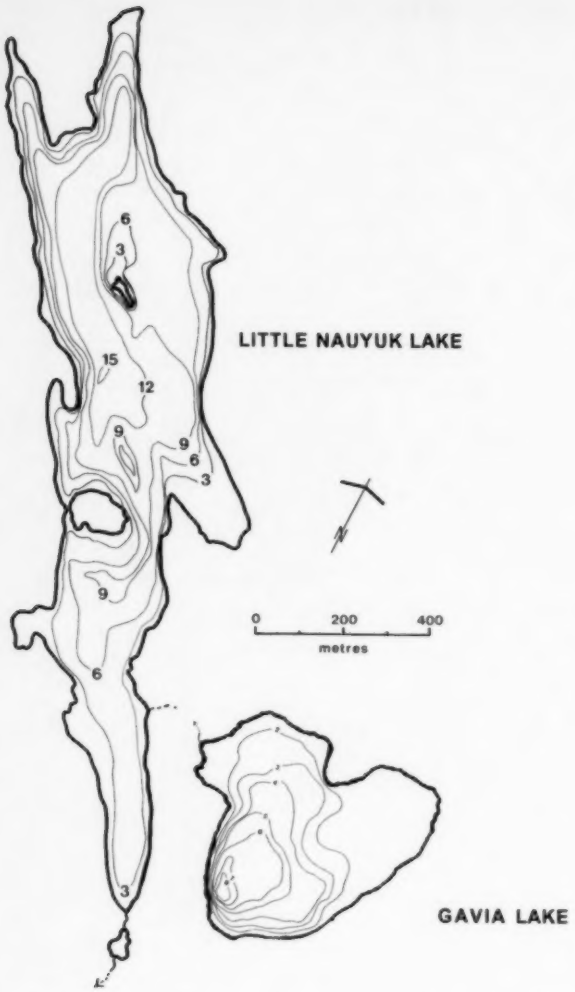

FIG. 1. Bathymetric map of Little Nauyuk and Gavia lakes on the Kent Peninsula, Northwest Territories.

in which a large number of juveniles declines in a negative logarithmic fashion as age and size increase (Beverton and Holt 1957; Ricker 1975). Although most fish population samples yield bell-shaped curves, this has been frequently considered to be the result of "gear selectivity": the proposition that a particular gear type will "select" a certain size of fish from a population consisting of a wide range of sizes.

Further, the evident stability of these fish populations did not accord with the diversity–stability hypothesis developed by MacArthur (1955) and Elton (1958). This hypothesis states that populations in simple systems tend to fluctuate whereas the populations of diverse systems are more stable. The regular fluctuations observed in small mammal populations of the tundra provided the main supporting evidence for fluctuation in simple ecosystems (Elton 1924, 1927; Elton and Nicholson 1942), while the perceived stability of tropical rain forests supported the notion that diverse systems are stable. Arctic lakes, being situated within the tundra biome, emphasized their nonconformity with the hypothesis. This conflict stimulated a search for an alternative explanation.

It was concluded that the reasons for the difference between the adjacent systems are (i) the high degree of lake autonomy compared with that of the open tundra, (ii) the severe climatic variability of the terrestrial system (both within and between seasons) is buffered by the physical properties of water and, (iii) the relatively homogeneous environment in the lakes.

Study Site

In 1974, an investigation into the life-history and productive capacity of Arctic char was initiated at Nauyuk Lake (68° 22′N, 107° 40′W) at the head of Parry Bay, on the Kent Peninsula, N.W.T. (Johnson 1989; Gyselman and Mohr 1990). The principle objective was to study the economically important anadromous Arctic char, but two small lakes close by, Little Nauyuk and Gavia lakes, provided an unparalleled opportunity to investigate simultaneously the effect of controlled perturbation on lake-dwelling Arctic char. The program started in 1974 and ran for 15 yr, terminating in 1988.

The Kent Peninsula and much of neighbouring Victoria Island emerged from the sea due to isostatic rebound approximately 8000 yr B.P., following the melting of the Pleistocene ice-sheet. Depressions in the land surface became lakes when the land rose above sea level; as the lakes gradually freshened, species in the preexisting fauna and flora either adjusted to the new conditions or suffered elimination. Many of the lakes eventually became completely isolated from the sea, as impassable falls developed as the land rose.

The initial premise was that the two experimental lakes, prior to the start of the experimental program, had existed in an ecologically stable state. This assumption was based on the previous experience at Keyhole Lake, as well as many other lakes in the Northwest Territories (Johnson 1983), but this assumption could not be tested without many years' delay.

The experimental lakes occur in a region of rocky dikes and sills along the northern coast of Parry Bay. Gavia Lake is approximately 70 m above sea level; it has the form of a relatively shallow bowl with a surface area of 17.4 ha and a maximum depth of 8 m (Fig. 1). The eastern shore slopes gently downward from a flat region of tundra to the deepest water on the southwestern side in the centre of a small rocky basin. In winter, ice cover reduces the water volume to 45% of its summer value. At this latitude the sun does not come above the horizon between December and January. Along the south shore, there is an area of broken rock and boulders about 100–200 m long. On the western edge the outflow drains down a rocky hillside into Little Nauyuk Lake. There is no naturally excavated channel.

Little Nauyuk Lake (approximately 35 m above sea level) lies in a long, narrow cleft in the rocks. It is 44.6 ha in area and has a maximum depth of 15 m. Much of the lake shoreline falls precipitously into the water from the surrounding cliffs. Only 14% of the surface area has water less than 2 m deep, which is the depth to which ice forms in winter. Ice cover reduces the lake volume to 66% of its summer value (Gyselman and Mohr 1990). Temperatures in June

are close to zero under the ice but rise to 2°C at a depth of 3 m. Oxygen levels at this time are close to saturation, indicating little winter depletion; they then become supersaturated for the remainder of the open-water season. The ice breaks up in the second or third week of July, following which temperatures rise quite rapidly to 7–8°C by the beginning of August. Maximum temperatures are reached in the third week in August. In the exceptionally warm summer of 1975 the lake was isothermal at 11°C on the 28 of August, but in the cool summer of 1978 the temperature on the same date was only 6°C. By the end of the first week in September the temperature is still 6–8°C, but ice usually begins to form again during the second or third week of the month. Both lakes are entirely devoid of emergent vegetation as a result of ice-scour.

Little Nauyuk drains directly to the sea down a series of small waterfalls, the water percolating into the gravel of the foreshore before reaching the ocean. There are no other tributaries to either of these lakes which are entirely dependent for their water supply on surface run-off in spring and seepage in the active layer of the tundra during the short summer. No groundwater enters these lakes, as they occur in an area of permafrost. There is no possibility of Arctic char stocks in either of these lakes being replenished from elsewhere.

For 9–10 mo of the year, these lakes, being completely encapsulated in ice, function as closed systems; sunlight is the only energy entering the system, photosynthesis being stimulated as soon as the sun reappears in February (Kalff and Welch 1974; Welch and Kalff 1974). Open water develops about 1 mo after the summer solstice, and the short ice-free period of about 60 d lasts until mid-September. Only during this period are the fish populations subject to predation, mainly by loons (*Gavia* spp.) and terns (*Sterna* spp.). Estimates of primary production were not made in these lakes, but Char Lake (74°C), close to Resolute Bay, Cornwallis Island, provided a value of 22 g $C \cdot m^{-2} \cdot yr^{-1}$, of which only 18% was produced in the water column, the remainder being benthic (Kalff and Welch 1974). Little Nauyuk appeared to be particularly oligotrophic, even within the context of arctic lakes.

The fish fauna of lakes in the vicinity is quite varied; for example, only Arctic char is found in Gavia Lake whereas Arctic char and ninespine stickleback (*Pungitius pungitius*) are present in Little Nauyuk Lake. However, other lakes at the same elevation above sea level have populations of lake trout and least (*Coregonus sardinella*) and Arctic cisco (*C. autumnalis*) but are devoid of Arctic char (Johnson 1980). As the lakes emerged from the sea, several species of "marine glacial relict" adapted to freshwater conditions (Johnson 1964). In Little Nauyuk Lake, these "relict" species make up a considerable fraction of the invertebrate fauna. They are the mysid *Mysis relicta* Lovén, the amphipod *Gammaracanthus loricatus aestuariorum* Lomakina, the copepod *Limnocalanus macrurus* G.O. Sars, and the large isopod (carapace length 30–40 mm) *Mesidotea entomon* (L.). Non-relict species include sphaerid clams, annelid worms, and various larval insects of which chironomids form the largest proportion. In Gavia Lake the only relict species are *L. macrurus* and *M. relicta*. Nauyuk Lake itself, which has access to the sea, and is considerably larger (27 km^2), has an additional relict species, the fourhorn sculpin (*Myoxocephalus quadricornis*) as well as containing Arctic char, lake trout, lake whitefish, and the two species of cisco.

In both lakes the food chain is relatively short. It has been studied in detail in Keyhole Lake (Vanriel 1989). The main part of the energy assimilated during primary production passes first through a detrital loop where the greatest fraction of the energy reserves is held. Bacterial action then provides food for the invertebrate fauna. Virtually all species of invertebrate present are consumed by the Arctic char which is the complete generalist in its food habits, occasionally even resorting to cannibalism. If the char avoids predators in its early life history stages, it lives out its physiological life span. Parasitism, (mainly *Diphyllobothrium* spp. and *Cystidicola* spp.) which is quite heavy in many char, has been studied in detail in these lakes (Black and Lankester 1984; Dick 1984).

Methods

Methods have been described in detail in Johnson (1983). Gill nets were the principal sampling device used; unfortunately, this type of gear always raises the spectre of "gillnet selectivity". In 1974, prototype experimental nets were used which consisted of a series of mesh sizes between 10 and 60 mm (bar measure). These nets were found to be very effective, although initial results created doubt about gillnet selectivity biassing samples over certain size classes. Therefore, to minimize this, the sampling gear was modified in 1975 by the addition of four mesh sizes between 10 and 33 mm to improve efficacy in the smallest size ranges. In all, 10 different mesh sizes between 10 and 60 mm were used. Together, these mesh sizes formed a close approximation to the ideal of a geometric series. The various mesh sizes were made up into two nets each 120 m long which were always fished as a pair. Together, the two nets formed one unit of effort; thus the combined catch from all mesh sizes yielded the catch per unit effort (c/ue) in terms of either number of fish or total weight. Nets were set at random throughout the lake and lifted approximately 20 h later. In 1975, 27 units of effort were fished (6.48 km); subsequently, between 6 and 8 units of effort were fished annually. An attempt to estimate initial population abundance was made by plotting declining c/ue against total removals (DeLury 1947, 1951).

In addition to gill nets, trap nets and hoop nets were used on a trial basis in Little Nauyuk Lake but with relatively small success, and little consistency. Electrofishing, where feasible, was carried out along the shoreline in both lakes. This extended the range of samples to lengths below 100 mm.

Fork length of all fish caught was measured in millimetres and weight was recorded in grams. For all fish, organisms in the stomach were recorded on a qualitative basis. Otoliths were removed from a set fraction of the total catch (usually one in five or one in three) and stored dry in envelopes to be read later in the laboratory. Ages were assigned according to the method of Nordeng (1961).

In Little Nauyuk Lake, a small test fishery in the first year was to be followed by heavy exploitation in the second and third years in order to impose a significant disturbance on the population; in year 4 and subsequent years the level was to be reduced to one that might possibly be sustainable. In the first 5 yr the fishery was carried out in two periods, one immediately after break-up in July and the other late in August. Changes proceeded slowly; each year produced new and interesting material so that annual sampling

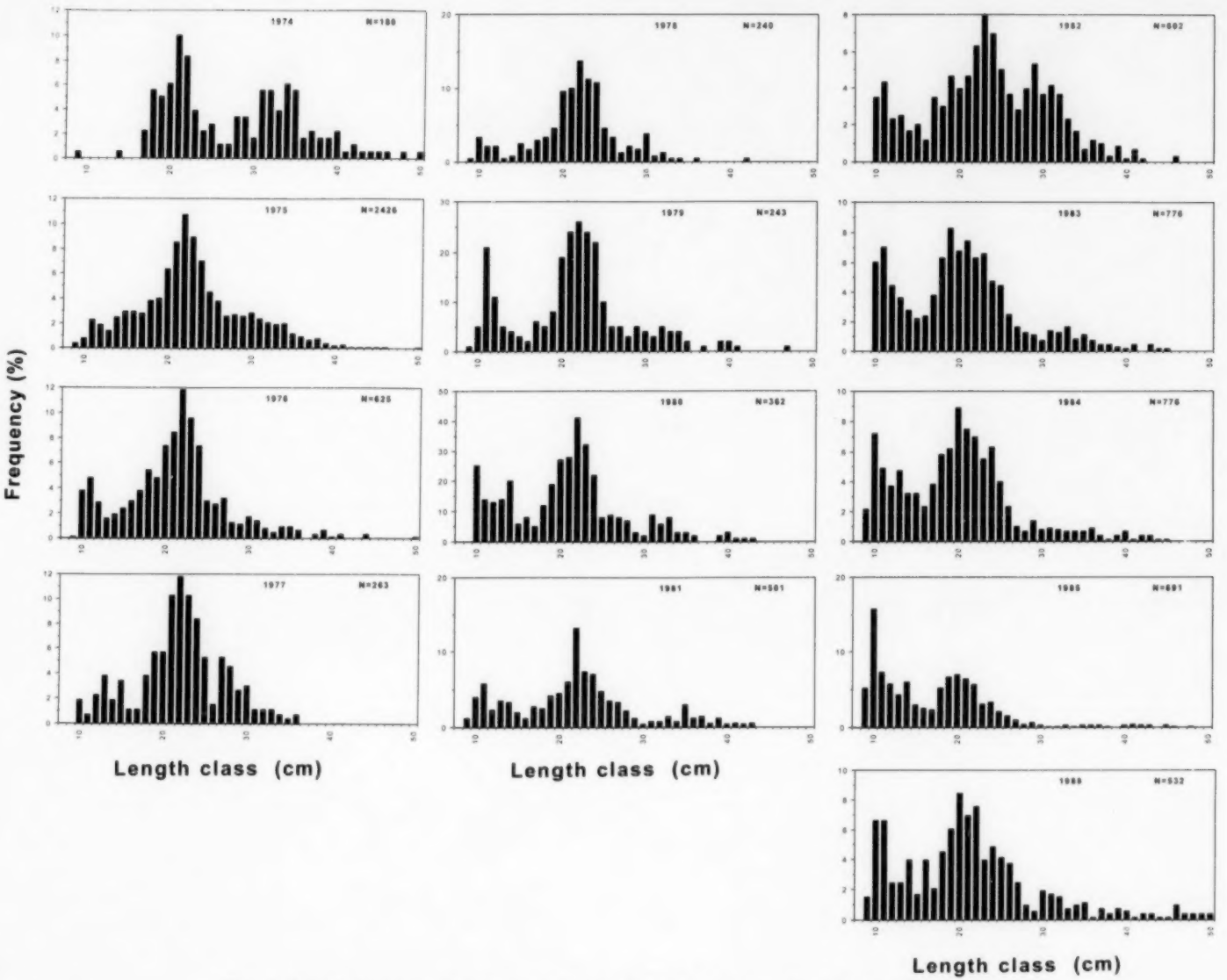

FIG. 2. Length–frequency distribution of catches of Arctic char, 1974–88, Little Nauyuk Lake.

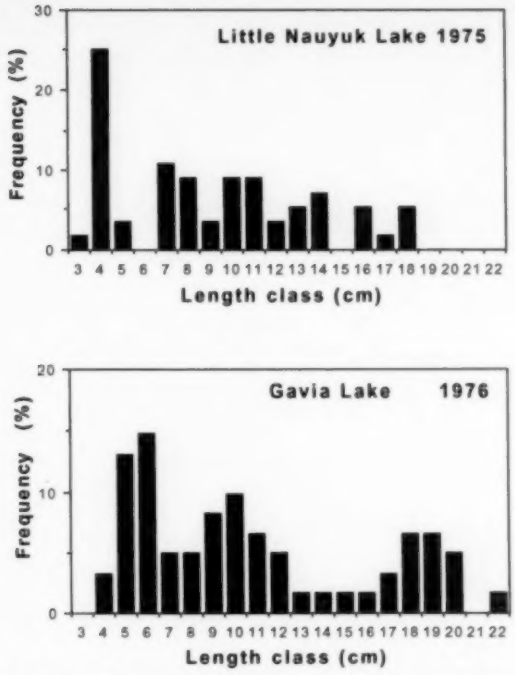

FIG. 3. Length–frequency distribution of Arctic char collected along the shorelines by electrofishing, Little Nauyuk and Gavia lakes.

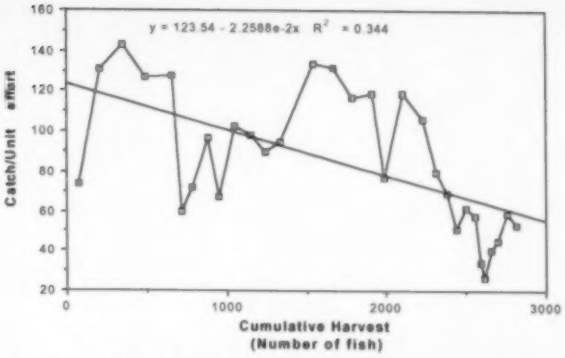

FIG. 4. The c/ue of Arctic char plotted against cumulative catch in 1975 and 1976, Little Nauyuk Lake. The estimate of the initial population was 4773.

continued in Little Nauyuk Lake at a relatively constant rate until 1980. After this date the level of exploitation was increased until 1985 in an effort to reduce the population to the greatest extent possible. Two years were then allowed to pass without sampling before the final observations were made in 1988.

The procedure to be adopted in Gavia Lake was similar, but without the heavy sampling in the second year. Fishing was to be at a relatively uniform level in order to observe the effects on stock structure of less aggressive exploitation. In this lake, annual sampling was terminated in 1981, followed by a gap of 1 yr until 1983, and then a four-summer interval before the final sampling in 1988.

Results

Little Nauyuk Lake

Population structure

Limited sampling in1974 indicated a population with a biomodal length–frequency distribution, with modes at 220 and 350 mm (Fig. 2). In the intensive sampling of 1975, a strongly unimodal configuration, with a modal value of 220 mm, was apparent. Contrary to the previous year, a significant mode at 350 mm was not clearly observable. In subsequent years, only a trace of a larger mode is evident.

In 1975, very few small fish (<150 mm) were taken during the intensive fishery in the early part of the season, but were much more abundant later in August (Johnson 1983). In 1976 the early fishery yielded a well-defined mode of small fish, with a modal value close to 120 mm. These fish, all aged 2 yr or more, were evidently in the population in 1975, although not available to the gear in the early fishery. In 1976 and subsequent years the small mode remained in evidence, gradually increasing in relative abundance as the number of fish (>150 mm) in the large mode declined.

The intensive fishery from 1981 to 1985 almost eliminated the main or "establishment" mode at 220 mm. Following 2 yr without fishing, the population showed strong signs of returning to its original configuration.

Electrofishing along the shoreline, particularly the rocky margins, yielded samples of small fish down to 40 mm (Fig. 3). These small fish were relatively rare. The most populous age group was 0+ (young-of-the-year) and the majority of these were 40 mm in length by mid-August.

Standing stock and yield

Although the abundance of fish, as measured by c/ue, declined greatly between 1974 and 1979 (Table 1), there appears to have been little effect on size distribution within the main mode. In general, c/ue tended to be quite irregular in the first 2 yr of intensive fishing, although a relatively rapid decline overall is indicated (Fig. 4). Even within the confines of Little Nauyuk Lake, an attempt to estimate initial abundance by the DeLury method of stock depletion (DeLury 1947, 1951) failed to give satisfactory results on account of highly variable catches, particularly in the late-season fishery. A first estimate, using all the catch records from 1975 and 1976, gave an initial population of 4773 (>150 mm) or 107·ha^{-1}. Alternatively, using only the early-season records from 1975 to 1980, which show a very regular decline in c/ue (Table 1), an almost straight line ($R^2 = 0.977$) was obtained, giving an initial population 6000 or 134·ha^{-1}. By the age structure and the regular decline in c/ue, there seems to have been relatively little recruitment before 1980. This result seems in general accord with the total removal of 10 503 fish in the 12 yr between 1974 and 1985. An overall mean weight of 115.1 g indicates an initial standing stock between 12.3 and 15.4 kg·ha^{-1}.

In Little Nauyuk Lake, a harvest of 2.1 kg·ha^{-1}·yr^{-1} was obtained over 12 summers (1974–85) and there is little indication that this level could not have been maintained indefinitely at about the 1980 level of 2.0 kg·ha^{-1}.

Age–frequency distribution

The changing age–frequency distribution is given in Fig. 5. Age–frequency appears, in general, to follow length–fre-

TABLE 1. General characteristics of catch, mean weight, and c/ue of Arctic char, 1974–88, Little Nauyuk Lake.

Year	Yield		Mean wt.	c/ue	
	No.	kg	(g)	No.	kg
1974	180	42.6	237.0	—	—
1975					
July	2436	324.5	132.2	101.7	13.5
Aug.	288	23.1	79.5	144.0	11.4
1976					
July	626	74.9	117.5	75.1	8.83
Aug.	229	25.0	109.4	78.0	8.53
1977					
July	263	30.4	115.7	65.5	7.55
Aug.	243	22.7	93.4	112.3	10.49
1978					
July	240	26.0	108.6	45.9	4.98
Aug.	434	34.6	79.8	138.0	10.93
Sept.	80	7.3	91.6	80.0	7.3
1979					
July	243	27.8	114.6	26.3	3.01
Aug.	301	30.0	99.7	76.5	7.56
1980	362	37.8	104.0	30.2	3.15
1981	501	67.8	135.3	42.5	5.60
1982	602	89.6	148.8	51.0	7.70
1983	713	76.4	107.3	118.0	12.70
1984					
July	795	75.5	95.0	132.5	12.59
Aug.	776	76.3	98.4	129.3	12.94
1985	691	48.6	70.1	172.8	10.83
1988	542	72.2	135.7	88.7	12.03
Total	10 545	1213.1	115.1	—	—

Initial population (1974) (char over 150 mm) = 4773 = 107·ha^{-1}
Total catch·ha^{-1} (1974–85)
Number = 236
Weight = 25.5 kg
Total catch·ha^{-1}·yr^{-1} (1974–85)
Number = 19.6
Weight = 2.13 kg

quency. Thus, although there is quite a good linear correlation between age and length as expressed in a conventional growth curve, there is a high degree of dispersion around the length at a given age (Table 2). This evidently results from the fact that individual growth is a monotonic function of age, but individuals grow at very different rates. Within each length group, there is a considerable range of age, with the greatest range invariably occurring in the modal length class. In 1975, individuals in the modal length class were between 5 and 20 yr of age. Ages appear to reside within an envelope that remains quite constant, although if the relative frequency of each age class within the modal length group is computed, the age of greatest abundance varies from year to year, apparently without regularity, but always within an envelope between the limits of 8 and 12 yr (Fig. 6). Despite these irregularities, the mean age of each length class remains quite constant (Fig. 7).

When a virtual population was constructed from all samples between 1974 and 1981, each year class was found to be remarkably uniformly represented (Johnson 1983).

Food preferences

Virtually all invertebrates present are food for the Arctic char: chironomid larvae and pupae are the dominant items, with caddis larvae, oligochaetes, *M. relicta*, *G. loricatus*, and sphaerid clams forming the bulk of the remainder. Sticklebacks are eaten rarely and there was a 2% incidence of cannibalism in char over 330 mm in length; 10% of stomachs examined were empty. The large isopod *Mesidotea* was found only in char over 280 mm in length, but fish of this length and above consumed it in considerable quantities.

Gavia Lake

Population structure

In 1974, there was evident bimodality in the sample (Fig. 8), but as indicated above, the question of gillnet selectivity could not be ruled out. One large char, 640 mm in length (not shown in the figure), dominated the catch statistics. The samples in 1975 closely approached the accepted configuration of a fish population, in which a relatively large number of fish in the smallest size category declines as age and size increase. There was little support for a bimodal structure although there is some indication of a mode at 190 mm. Annual and total catch and yield per hectare are given in Table 3.

In 1976, a dramatic change was indicated by the assumption of a unimodal length–frequency distribution, with a modal value between 190 and 200 mm. The absence of fish in the smallest sizes, so abundant in the previous year, is

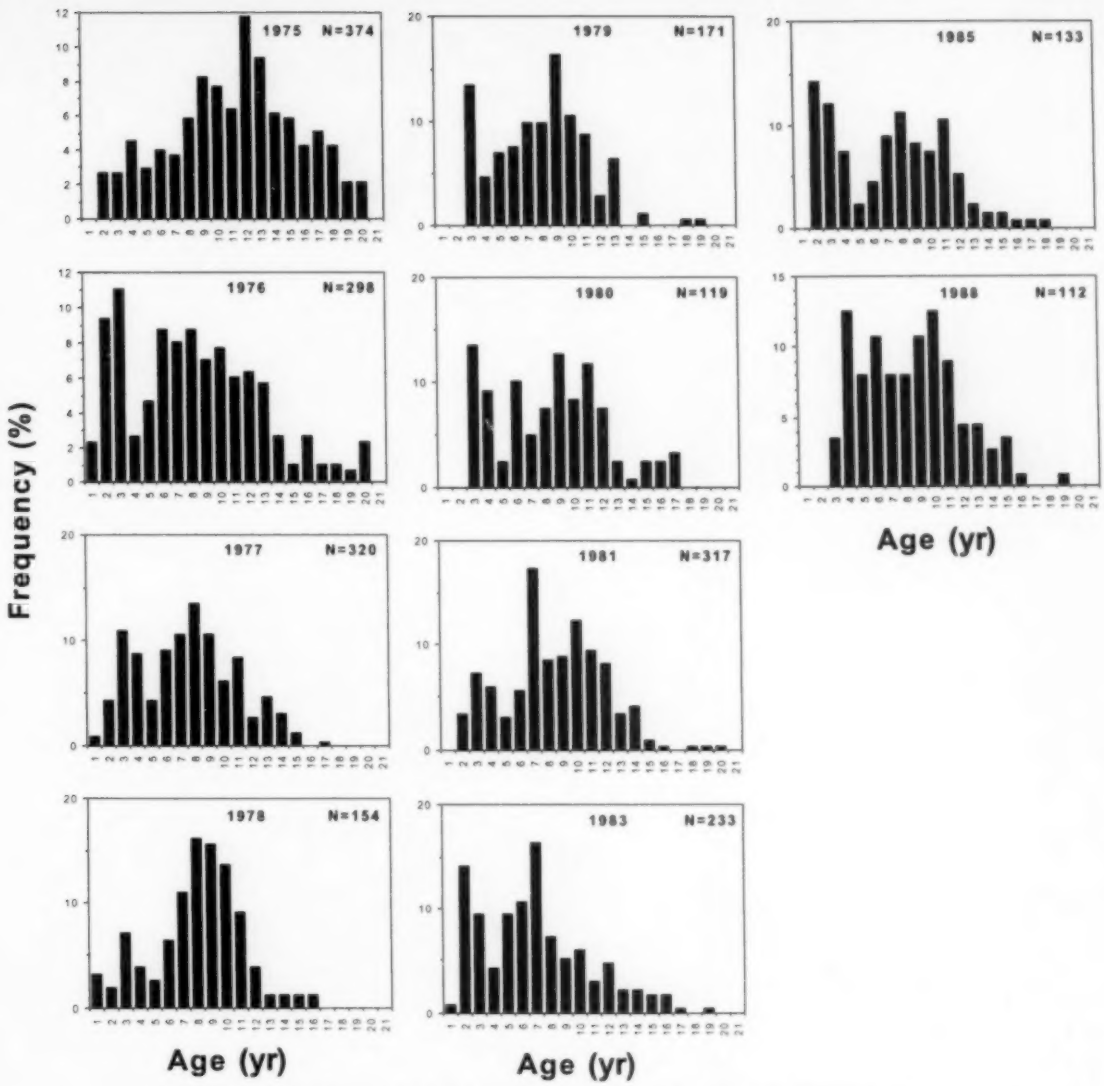

FIG. 5. Age–frequency distribution of Arctic char, 1974–88, Little Nauyuk Lake.

remarkable. This modal structure, which developed in 1976, remained constant over the subsequent years of the fishery as abundance declined. After 1976, the fishery, as in Little Nauyuk Lake, developed a mode of small fish. This mode had a modal value of 100–120 mm which remained constant in value although fluctuating considerably in magnitude until 1983. After 4 yr without sampling, the stock structure in 1988 had reverted to a condition very close to that indicated in 1975.

Age–frequency distribution

Age–frequency, to a considerable extent, followed length–frequency (Fig. 9). In 1975 the distribution showed a large number of fish in the 4- to 5-yr age classes followed by a relatively regular decline in abundance as age increased. The maximum age of an individual fish was 17 yr. In the following years, age tended to be unimodal, although, with the exception of the year 1977, the distribution was by no means as regular or as well defined as that for length. Within each length group, there was a very wide dispersion of age, the greatest spread again being reached in the modal length group. In 1975 the range of age in the 190- to 200-mm length group was from 7 to 13 yr. When the numbers at each age within each length group are arranged in a matrix, the population as a whole, as in Little Nauyuk Lake, appears to exist within an envelope, the shape of which does not appear to vary greatly from year to year (Table 4). On the other hand, the specific age composition within each length class may vary considerably with little discernible regularity.

Electrofishing in 1975, along the rocky southern shore, showed the existence of a number of small fish (<100 mm) as well as a mode at 180 mm (Fig. 4).

TABLE 2. Age– and length–frequency matrix for Arctic char, 1975 and 1979, Little Nauyuk Lake. There appears to have been very little change in the structure of the population despite severe stock depletion, as witnessed by the decline in c/ue. Ages and lengths lie within an envelope of relatively constant shape.

	Length class (5-cm intervals)											
Age	0–5	5–9	10–14	15–19	20–24	25–29	30–34	35–39	40–44	45–49	>50	Total
1975												
30											1	1
29												
28												
27												
26												
25									1		2	3
24										1		1
23											2	2
22								1	1			2
21							1					1
20					1		1		1			3
19					1		3	3	1			8
18					1		6	3	4	1	1	16
17					3		8	5	4			20
16					5	1	4	7	1			18
15					6	1	10	4	1			22
14					7	4	9	4				24
13				1	19	5	10	2				37
12					26	10	8	1				45
11				2	19	4	2					27
10				2	13	10	5	1				31
9			2	2	21	8	1					34
8				6	9	8						23
7				8	5	1						14
6			2	10	5							17
5			4	9	2	1						16
4			12	5								17
3			12	2								14
2	2		12									14
1												
0												
Total	2	0	44	47	143	53	68	31	14	3	5	410
1979												
20								1				1
19									1			1
18												
17												
16									1			1
15												
14					6	3	1		1			11
13					4		1					5
12				2	9	2	1	3				17
11					14	2					1	17
10					16	5	6	1				28
9				1	11	5	1					18
8				1	12	1	3					17
7				2	8	2						12
6			1	4	4	3						12
5			1	6	5							12
4			6	2								8
3			22	1								23
2												
1												
0												
Total	0	0	30	19	89	23	13	5	3	0	1	183

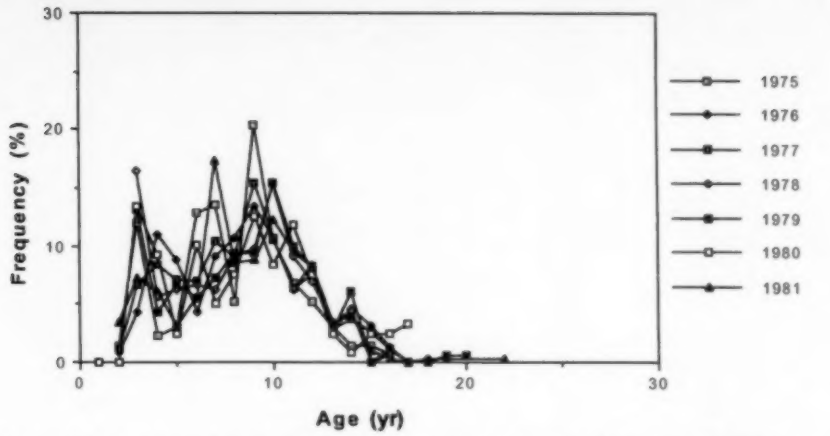

FIG. 6. Relative frequency of each age class of Arctic char within the modal length class, Little Nauyuk Lake. The maximum frequency changes from year to year apparently without order, but always occurs between the ages of 8 and 12 yr.

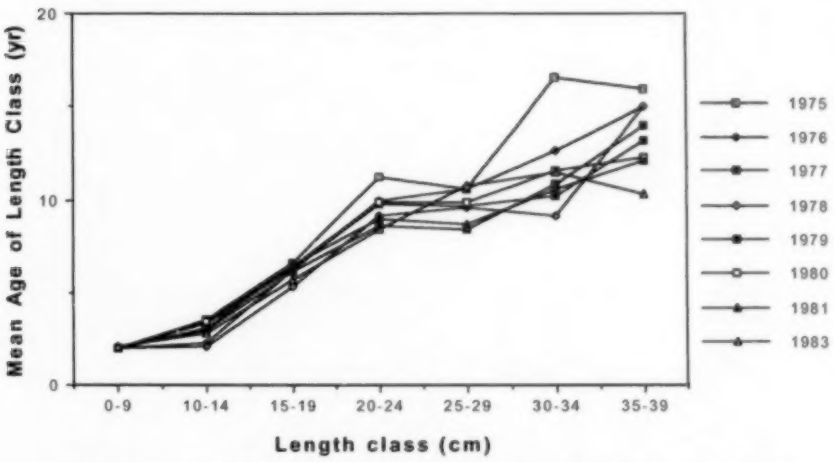

FIG. 7. Mean age of each age class of Arctic char, 1975–83, Little Nauyuk Lake.

Discussion

The faunal difference between the two experimental lakes, and others in the vicinity, most probably results from the differential elimination of species during their formation (Johnson 1980). Neighbouring lakes have somewhat different faunas, but the fauna of each lake is invariably a subset of the full set of organisms found in those large lakes in the vicinity (such as Nauyuk Lake itself) which have maintained access to the sea. This set most probably formed the initial founder complex of species for all lakes in the region, from which each lake, owing to its specific physical limnology, "selected" the appropriate subset. This reduction in species richness, as one or a few species assume dominance, is comparable with the elimination of plant species in the terminal stages of the successional process (Johnson 1994).

In both lakes the mean size of fish is quite large (190–220 mm) when compared with other organisms in the system, or by comparison with Arctic char in Char Lake, Cornwallis Island (≈130 mm) (Johnson 1983), or Lake "A", Borup Fiord (≈90 mm) (Parker and Johnson 1991), but small when compared with char in lakes such as Keyhole Lake (modal value ≈300 mm) or Nelson Lake, Cornwallis Island (≈350 mm). These differences cannot be attributed to altitude, for populations of both small and large fish exist at similar latitudes in Borup Fiord, Cornwallis Island, and Nauyuk Lake. In Scandinavia, Arctic char is noted for its ability to form dense populations of "dwarf" fish (Amundsen 1989; Klemetsen et al. 1989). Size thus appears to be very flexible in this species and very responsive to environmental conditions.

The estimated initial standing stock in Little Nauyuk Lake of between 12.3 and 15.4 $kg \cdot ha^{-1}$ is slightly above the 9.23 $kg \cdot ha^{-1}$ (fish over 130 mm in length) determined for Char Lake (some 7° of latitude further north) (MacCallum and Regier 1984), but well below the 44 $kg \cdot ha^{-1}$ estimated by Hunter (1970) for Keyhole Lake, at about the same latitude as the experimental lakes. These values compare closely with those many temperate lakes. The harvest of 2.13 and 1.6 $kg \cdot ha^{-1} = \cdot yr^{-1}$, respectively, for Little Nauyuk

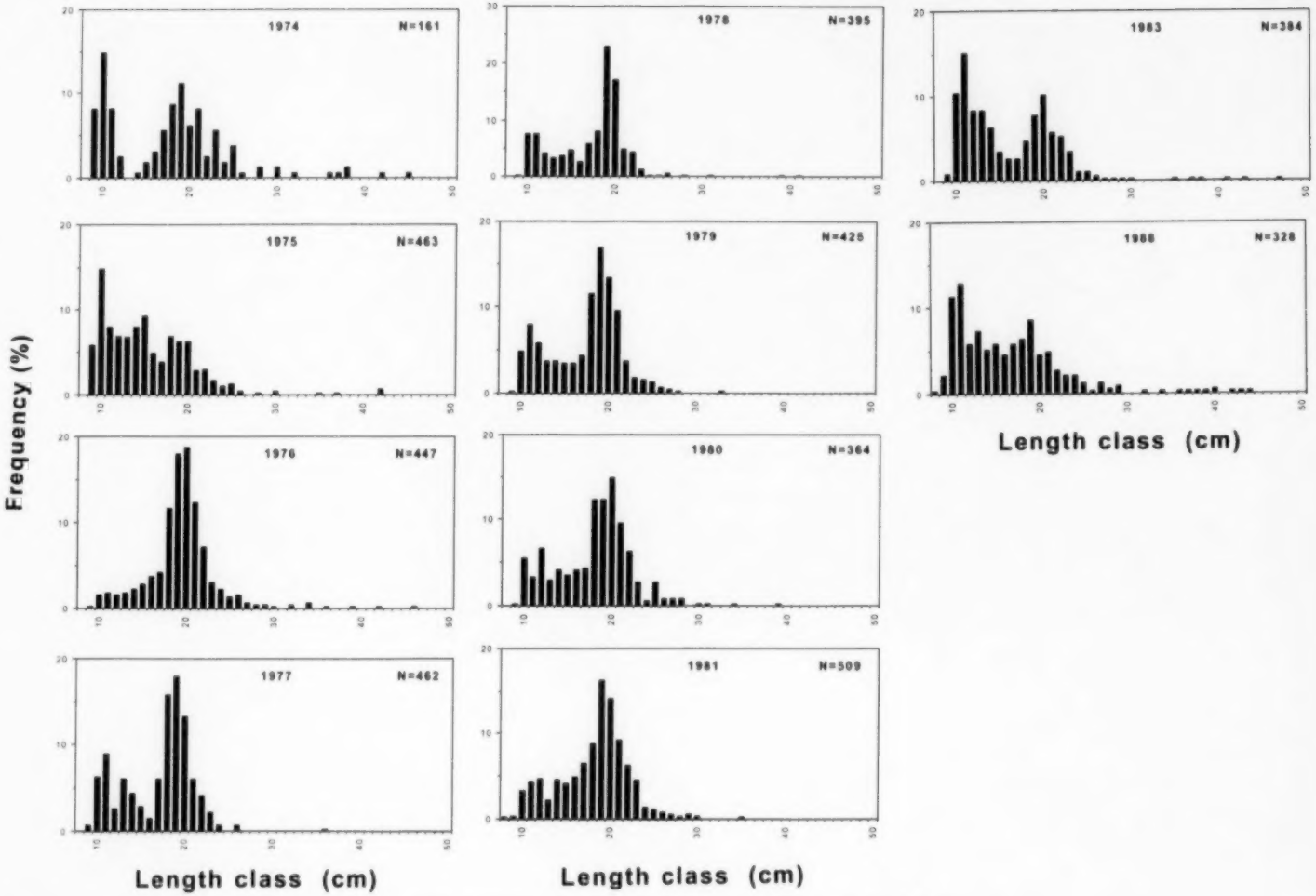

FIG. 8. Length–frequency distribution of Arctic char, 1974–88, Gavia Lake.

TABLE 3. Characteristics of catch, mean weight, and c/ue in samples of Arctic char, 1974–88, Gavia Lake.

Year	Yield		Mean weight (g)	c/ue	
	No.	kg		No.	kg
1974	164	15.8	123	164	15.8
1975	393	16.0	40	160	10.3
1976	447	34.9	79	166	13.0
1977	467	23.3	50	94	4.7
1978					
July	397	24.0	61	84	5.1
Aug.	191	8.6	45		
Sept.	311	17.6	57		
1979	425	24.1	69	53	3.0
1980	365	25.0	69	46	3.1
1981	509	36.3	71	127	9.1
1983	384	20.8	52	192	10.4
1988	358	25.1	70	89	6.3
Total	4406	271.5	62		

Total catch·ha^{-1} (1974–81)
Number = 210
Weight = 12.9 kg
Total catch·ha^{-1}·yr^{-1} (1974–81)
Number = 26
Weight = 1.6 kg

TABLE 4. Age– and Length–frequency matrix for Arctic char, 1975, Gavia Lake.

Age	Length class (5-cm intervals)									
	5–9	10–14	15–19	20–24	25–29	30–34	35–39	40–44	45–49	Total
16							1			1
15				1	1					2
14					1	1		1		3
13			1		1	1				3
12					2		1			3
11			1			1				2
10			1	2	1					4
9			1	2	1					4
8				2	1					3
7			3							3
6			2							2
5		2	8							10
4		9	2							11
3	1	5								6
2		5								5
1										
Total	1	21	19	7	8	3	2	1		62

and Gavia lakes is, despite very low primary production, also comparable with that of lakes much further to the south. The high standing stock relative to the low primary production, equivalent to a low production to biomass ratio (*P/B*), is attributed to the simplicity of the system with its short, direct food chains.

The most significant result of this experiment is the manner in which the Arctic char populations meet the criteria for stability established by Hurd et al. (1971) and Connell and Sousa (1983). Both lakes were strongly perturbed and both returned to a state very close to their original configuration without significant oscillation. As the stability of an ecosystem as a whole is largely characterized by the dominant species (Frank 1968), it may be concluded that the lake system too can be regarded as stable. This closely reflects Forbes' (1887) view expressed in "The lake as a microcosm".

Stability in arctic lakes, where the terminal predator is the dominant species, has much in common with the "climax state of forest ecologists (Whittaker 1951, 1953), despite the fact that in a forest the dominant species is also the main primary producer. It is therefore concluded that an autonomous ecosystem proceeds toward an equilibrium state when environmental conditions permit. Two stable states are allowable, one in which the dominant species is terminal in the food chain and the other in which the primary producer is dominant.

Stability in the experimental lakes, far from fostering maximum diversity, appears to have necessitated a reduc-

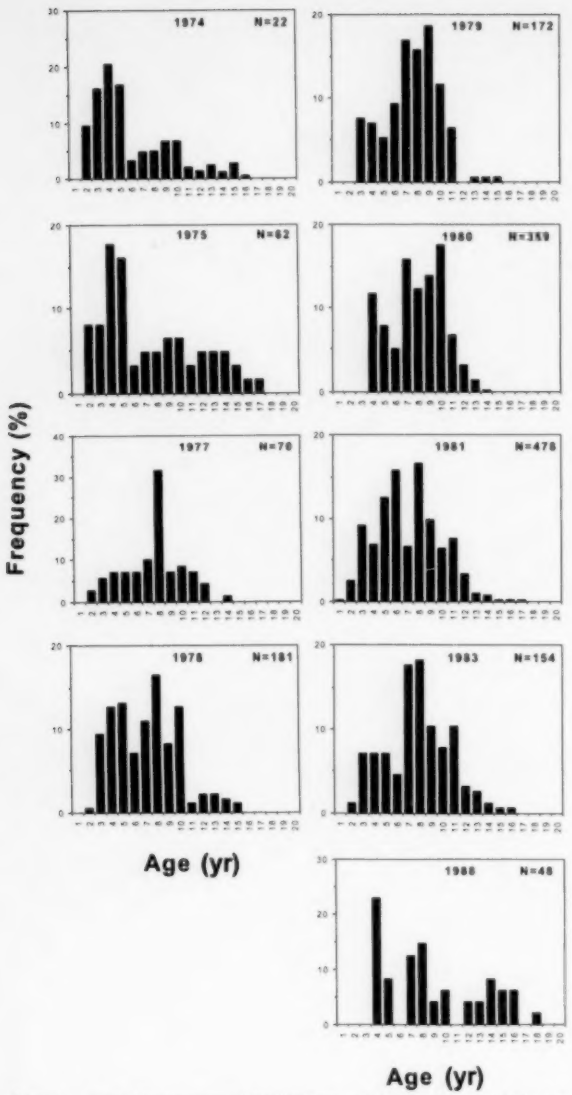

FIG. 9. Age–frequency distribution of Arctic char, 1975–88, Gavia Lake.

tion in the number of species, compared with the total number available, with each lake "selecting" those which it can support.

In conformity with Hurd et al.'s (1971) characterization of stability, the char population in Little Nauyuk Lake in the early stages of disturbance strongly resisted deformation, retaining its original configuration over many years, despite declining abundance. The amplitude of deflection must be adjudged comparatively small compared with the deflecting force. The rapidity of the response is relatively fast also, full recovery from the imposed state being estimated at about 6–8 yr. Both populations exhibit a strong damping mechanism, expressed in the control of recruitment and the maintenance of a high degree of uniformity in the "establishment". Stability as characterized by Hurd et al. (1971) also allows "resilience" to be characterized. Resilience is the resultant of the rapidity of the response to perturbation and the rate at which the deflection is damped. However, these two characteristics act in opposition; a rapid response demands a high level of recruitment to the establishment whereas damping demands slowing of recruitment to prevent overshoot. A resilient species is therefore one with a nice combination of these two characteristics: one that allows rapid but well-damped progression to the final position.

The initial fishery in Little Nauyuk Lake in 1974–75 indicated the presence of very few juvenile fish. But as the population in the establishment declined, a mode of juveniles appeared with a modal value of 110–120 mm. By their ages, these fish were present at the start of the operation, only appearing in 1976 when a significant fraction of the larger fish had been removed. Thus, it is hypothesized that recruitment is controlled by suppression of the juvenile phases.

The modal configuration is too regular in its occurrence to be dismissed as an anomaly resulting from inadequate methodology or "gear selectivity". This conclusion is supported by (i) the modal size of char caught by the same gear varies greatly between lakes while the modal size in each lake remains constant, (ii) the manifest ability of the gear to catch fish of all sizes down to 100 mm, when they are actually moving in the water column, and (iii) the impossibility of fish movement between lakes. However, there can be no escape from the principal that every year class declines in abundance monotonically with time, although the notion that a population in a stable state, at a single point in time, represents a year class over its life span requires considerable modification.

The modal structure, given the ages of the component individuals, is dependent on coherence within the population. Such a structure could not be maintained without interaction between individuals. This interaction results in uniformity, to a large degree independent of age. A similar manifestation of coherence is observed in schooling fishes where members of a particular school are all of the same size (Shaw 1970).

The appearance of juvenile fish in the net catches, only after a reduction in population density of the establishment, indicates suppression of small fish, through their relegation to the periphery of the habitat. That they are there is shown by electrofishing, although the proportion of small fish relative to the large population cannot be determined. This behavioural pattern ensures control of recruitment which forms part of the internal damping mechanism necessary to maintain stability within the population. This mechanism presupposes a "stack" of potential recruits of variable age, maintained in the peripheral regions of the habitat by suppressional effects. When opportunity occurs, an individual of relatively small size but variable age enters the establishment space and grows rapidly toward modal size (Johnson 1976). Other individuals, which do not have the opportunity to advance to the establishment, remain small in size and vulnerable to bird predation. Such a mechanism seems necessary to support the observed length– and age–frequency distributions, which show order at the population level but apparent disorder at the individual level. Following one year class over its life span shows both an apparent increase and a decrease in abundance over the years.

Segregation with respect to size is evidently a fundamental component of Arctic char behaviour, size precedence having been observed in the migration of anadromous Arc-

tic char both to and from the sea (Johnson 1989). Not only do juveniles migrate after the completion of the adult run, but within the adults, it is the largest fish which move first. In the Firth River in the Yukon in winter, large char occupied the central region of the stream where flow was greatest, while small fish clustered along the margin where ice and streambed meet (Glova and McCart 1974).

Gavia Lake provides an instructive and, to date, unique comparison. In 1975 the population structure closely approached that of the conventional negative logarithmic distribution: there was a large number of small fish, a declining number of intermediate-sized fish, and a single very large specimen of 640 mm. However, this configuration appeared to be unstable to fishing pressure. By 1976, the largest fish having been removed preferentially by the sampling procedure on account of their greater freedom of movement, a strongly unimodal distribution developed. The change, surprising in its rapidity, occurred over the course of one winter. In subsequent years, a bimodal configuration developed, similar to that observed in Little Nauyuk Lake which was maintained for the remainder of the exploitation phase. Evidently the modal structure is much more robust with respect to the fishery than the original hierachial one. Nevertheless, in the closing stages of the experiment, 5 yr after regular fishing ceased, the original structure had almost returned.

Thus, there appear to be two distinct levels of stability in this lake: (i) a hierarchical "ground state", relatively unstable to an external perturbation, and (ii) a relatively uniform length–frequency distribution, stable to external perturbation, and maintained by selective removal of the largest fish in the population.

The reason for this unusual structure in Gavia Lake can only be speculated upon. Possibly the environmental conditions at some stage in the seasonal cycle preclude the full functioning of the cohesive mechanism, instead favouring a few large fish. Conceivably, this is during winter when the habitat is reduced to 45% of its summer volume by the formation of 2 m of ice. Conditions at this time must be relatively stressful, given the increased concentration of stock and the dominating behaviour of large fish. The elimination of these large fish evidently removes a factor preventing the remainder of the population from asserting its natural propensity to equalize stresses and uniformly partition space and food. Cannibalism may also be a contributory factor in maintaining asymmetry within the population, although the incidence of cannibalism in Arctic char populations is low.

From the evidence in Gavia Lake, it appears that under certain conditions the uniformity and coherence maintained by symmetrical interaction break down and a hierarchy is formed, which is relatively unstable to external perturbation.

A theoretical requirement for stability is that it be characterized by some physical state. In Little Nauyuk lake and many lakes with a similar configuration, the stable endpoint can be designated a state of "least specific dissipation". This tendency to least dissipation is a population characteristic which functions as a damping mechanism. The theoretical requirements for a state of least dissipation in a population in which the individuals have a less than infinite life span are (i) the equipartitioning of the available free energy, through symmetrical interaction among individuals, as demanded by the doctrine of homeokinesis (Soodak and Iberall 1978; Johnson 1994), (ii) modulation of individual growth rate by the population, (iii) desynchronization of individual life history to avoid fluctuations in abundance, (iv) the absence of predation (epidemics or other major disturbances) allowing the attainment of maximum age and maximum biomass, (v) control of recruitment at population densities less than maximum, and (vi) reduction in species diversity. As damping is a population attribute, least dissipation depends on cohesion among the interacting individuals: coherence demands communication, and as Prigogine and Stengers (1984) stated, communication "may in fact be taken as the very basis of the definition of a biological system."

Least specific dissipation implies that the maximum time delay possible is imposed on the assimilated free energy (energy capable of doing work). When it is no longer capable of performing work, it is dissipated as heat. That is, unit biomass is maintained by the smallest energy flow possible, within the prevailing physiological and environmental limits. Under the appropriate conditions, biomass increases through the conservation of free energy, attaining maximum value when greatest attainable age and size have been reached.

This is evident on physiological grounds because (i) the larger the individual size, the lower the specific metabolic rate (Kleiber 1932) and (ii) the smaller the number of juveniles, the less the energy required to support rapid growth. Least dissipation implies the absence of fluctuation in abundance over time and a return to the ground state when the disturbance ceases (Prigogine 1978). The dominant species, being relatively free from predators, and being confined within the system boundaries, is the species which most closely approaches the physiological and environmental limits.

The "principle of least time" is a physical principle developed by the French mathematician Pierre de Fermat in the seventeenth century. This principle states that the path taken by a light ray through transparent media is characterized by the shortest time possible; this path is not necessarily a straight line. This principle was subsequently expanded and applied to mechanical systems in the "principle of least action" (Feynman 1963; Watson 1986), where action has the dimensions of energy *times* time. This principle, if of general application, runs counter to the observed trend to least dissipation. "Least dissipation" is equivalent to a state of "*most* action."

Therefore, it is hypothesized that ecosystems are structured on the opposition of two nearly equal forces, one tending to time-delay energy flow through the ecosystem, giving rise to a state of least dissipation (the "principle of most action") and the other tending to accelerate energy flow (the "principle of least action"). Existence and continuity therefore depend on the immediate supremacy of the trend toward least dissipation. In an ecosystem far from the stable state or climax, successional processes gradually equalize the forces until a state of no change is reached. The origin of the "most action" principle is discussed elsewhere (Johnson 1994).

Energy flow rates are accelerated through increased diversity (as observed over evolutionary time), leading to more intensive heterotrophy. Dominance of the trend to least dissipation is evident in the elimination of species in the formative stages of the lake ecosystem. Interaction between

the two nearly equal forces leads to greater individual complexity and a more complex hierarchical structure (Johnson 1994).

Energy flows are stabilized at the climax by this "homeorhetic" process: the stabilization of flows (Waddington 1968). It is not a homeostatic process as proposed earlier (Johnson 1983) because homeostasis implies the maintenance of a specific state as, for example, a constant pH of the blood. Homeorhesis allows fluidity and change, enabling systems to adjust and adapt to the prevailing environment over a very wide range of conditions.

Initially, a leap of faith is required to accept the universality of action principles. However, once accepted, their application illuminates many accepted facets of ecosystem structure, from the increase in *P/B* along the food chain (Winberg et al. 1972; Saunders et al. 1980), the decrease in *P/B* with declining latitude (Mann and Brylinsky 1975), to *r*- and *K*-selection (MacArthur and Wilson 1967). Succession is the interplay of the opposing forces over time as a displaced system moves toward equilibrium. At any point in time, an ecosystem will tend to move in the direction of the specific climax for that particular environment and complement of species, but should either species or environment change, there will be a change in the projected climax and the system will move off in the direction of the new (projected) climax. If the environment shifts beyond the limits of accommodation, the system responds by making the necessary adjustments to biomass and diversity. As seen in neighbouring arctic lakes, one species may be substituted for another in comparable environments. It is not a particular group of species that is important in the formation of an ecosystem hierarchy: the biological imperative is that the species "selected" from those "available" dispose themselves in a functional homeorhetic system.

All species in a stable ecosystem may be viewed as undergoing damped oscillations around a mean value, within a hierarchical order established by the differential capacity of the assembled species to conserve free energy (i.e., increase in "action" or decrease in *P/B*). This capacity functions as a damping mechanism on species and ecosystems. The dominant species is maximally damped, hence assumes a position at the head of the hierarchy; the remaining species fit themselves into the hierarchy as best they may. When the climax state has been reached, the system as a whole as well as the dominant species reaches a state of "least specific dissipation" appropriate to the specific assemblage and environment. This interpretation implies that the basic characteristic of all species populations and ecosystems is that they are *stability seeking*, although they may in fact be maintained far from the stable state by extraneous forces. The actual degree of stability achieved will depend on the degree of system autonomy, the environmental variability, and the inherent damping capacity of the individual species.

Over evolutionary time the various subsystems of the world seek stability within the essentially closed system of the biosphere. Without such characteristics, it is difficult to see how a system could survive and maintain continuity over long periods of time and, simultaneously, adapt to new conditions in a world where change and fluctuation never cease.

Perhaps Linnaeus was right in that we do need a new science built around the concept of homeorhesis, the balance of energy flows in nature.

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I particularly thank Charlie Kiyok of Nauyuk Lake, who first showed us Little Nauyuk Lake, and assured us that it contained Arctic char. Charlie and his family shared their knowledge with us and tolerated our presence with good humour and sometimes amusement. Over the course of the years, they assisted greatly in making our stay both interesting and enjoyable. In other spheres, I thank Scott Campbell, John Babbaluk, Max Blouw, and Karl Kroeker who were instrumental in getting the project started and Eric Gyselman and Bonnie Burns who did so much to maintain the momentum. Also, I thank the many summer assistants who contributed much to the success and enjoyment of the project.

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Pattern and Process in Ecological Systems: A Step in the Development of a General Ecological Theory

Lionel Johnson[1]

Department of Fisheries and Oceans, Freshwater Institute, 501 University Crescent, Winnipeg, MB R3T 2N6, Canada

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The dominant fish populations in undisturbed arctic lakes are characterized as being in a state of "least specific dissipation": the greatest biomass attainable for a given energy input. A survey of autonomous ecosystems in various parts of the world indicated that this pattern is widespread. It is concluded that ecosystems are formed at the point of intersection of two established physical principles: the "principle of most action" (≈least dissipation or conservation of free energy) and the "principle of least action". "Action" is defined as the product of energy *times* time (joule-seconds). The trend to "most action" necessitates deceleration of energy flow: "least action" accelerates energy flow. For an ecosystem to survive over ecological time, the principle of most action must override the principle of least action. In that different species of organism have different capacities to conserve free energy (increase action), a hierarchy is formed locally in which action increases at each hierarchical level. Over the long term, as a result of genetic instability, both principles induce change, but the principle of least action dominates system behaviour causing increasingly rapid energy dissipation. Evolution is the resultant of these two countervailing forces.

Les populations de poissons dominantes dans des lacs arctiques vierges sont décrites comme en état de « moindre dissipation spécifique » , c'est-à-dire la biomasse maximale pour un apport énergétique donné. Une étude des écosystèmes autonomes dans différentes parties du monde a indiqué que ce profil est répandu. On en conclut que les écosystèmes sont formés au point d'intersection de deux principes physiques établis, soit le « principe de l'action maximale » (≈la moinde dissipation ou la conservation de l'énergie libre) et le « principe de la moinde action ». L'« action » est une grandeur ayant les dimensions d'une énergie multipliée par un temps (joule-secs). La tendance à l'action maximale exige un ralentissement du transfert d'énergie : « la moindre action » accélère le transfert d'énergie. Pour qu'un écosystème puisse survivre au temps écologique, le principe de l'action maximale ne doit pas tenir compte du principe de la moindre action. En ce sens que différentes espèces d'organismes dotées de différentes capacités de conserver l'énergie libre (augmenter l'action), une hiérarchie se forme localement dans le cadre de laquelle l'action augmente à chaque niveau hiérarchique. À long terme, à cause d'une instabilité génétique, les deux principes induisent des changements, mais le principe de la moindre action domine le comportement du système ce qui provoque une dissipation de l'énergie de plus en plus rapide. L'évolution est la résultante de ces deux forces compensatrices.

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The great deficiency in present-day ecology is the lack of integrative principles on which to build a sound approach to the living world. Without such principles, based on accepted canon law, we shall never be able to develop a philosophy of biology that will lead us out of our present agonising environmental dilemma. The trenchant words of Ken Watt (Watt 1971), onetime scientist with the Ontario Department of Lands and Forests, are just as relevant today as when they were first uttered over 20 yr ago:

> If we do not develop a strong theoretical core that will bring all parts of ecology together we shall all be washed out to sea on a giant wave of unrelated information.

Despite this repeated warning (MacFadyen 1975; Southwood 1977), the tidal wave gathers offshore as more and more unrelated facts are amassed.

Given the present disconcerting state of many of our fisheries and the amount of effort that has been put into managing them, the most pertinent question that we, as biologists, should ask is: why has ecological theory to date so often failed to provide an adequate basis for their management causing managers to turn more and more to empirical or political solutions to biological problems? I do not think that in fisheries, we are alone in this, for most branches of applied ecology labour under similar difficulties. It is evident that we need a better understanding of fundamental biological processes and a clearer appreciation of man in his biological role. I believe that the conceptual models we have developed are not commensurate with the magnitude and complexity of the real situation, nor, frequently, do they reflect or incorporate many pertinent observations from the field.

[1]Present address: 10201 Wildflower Place, Sidney, BC V8L 3R3, Canada.

We need to stand back and take a fresh look at our problems, dismissing some, if not all, of our preconceived ideas. Perhaps we should take a lesson from the revolution in systematics that has occurred in recent years through the attempt of Cladists and Pheneticists to develop a theory-free system of classification (Hull 1988). Both schools renounced the theory-laden methods of evolutionary systematics with the aim of deriving a system of classification based on affinities, determined, as they believe, completely objectively. Throwing out fundamentals such as natural selection seems strange to many of us (according to some distinguished systematists, it is also wrong-headed) brought up in the traditional belief that a natural system of classification based on Darwinian principles is the true and only path. Such a housecleaning is essential on occasion and, even if one eventually returns to the familiar clutter, the house is likely to be viewed with renewed wisdom and affection.

Pattern and Process

The search for theory demands abstraction of the relevant patterns occurring in nature. Patterns are the emergent properties of systems, abstracted by the objective and imaginative grouping of observed characteristics. Process is the mechanism whereby such patterns are generated and maintained. Therefore, we must identify patterns before we can identify process, and process, as identified, must indicate where new and interesting patterns may be sought.

One of the continuing problems in fisheries research is that it has been highly process oriented but low on pattern. That is, many of the basic tenets of fish population dynamics are heavily theory-laden, although insufficiently based on observed pattern. Our determination to explain has overridden our knowledge of the patterns to be explained. This is understandable in light of the difficulties of obtaining accurate and complete information on exploited fish stocks and our Newtonian upbringing which imposes a rather rigid logic on cause and effect.

Relatively few ecologists have taken the determinedly empirical approach pioneered by Rigler (1975), although Peters' (1983) work on body size and that of Yodzis (1982), Briand (1985), and Cohen (1989) on food webs and compartmentation of ecosystems follow a similar path. To many ecologists, these avenues appear rather sterile because they lack the exciting element of process. Without process, we merely collect and arrange facts. Without theory, the mere collection of facts runs the danger of becoming simply biological voyeurism. Therefore, I believe, we need to examine the relative place of each species in the ecosystem and review the emergent patterns of population structure in a theory-free manner. Process, when developed, must, ultimately, be testable through observation and carefully designed experiment.

In the Arctic, it has been possible to examine lake ecosystems that have had a sufficient length of time free from disturbance, either natural of man-made, to have reached an end-point, at least within the relatively short-term geological time frame of about 10 000 yr. These systems are no longer in a transitional state, as is the case with most ecosystems today, where man's activities impose continuously changing and challenging conditions.

The Stimulus for a New Approach

The first hint of impending disillusion with accepted concepts arose when apparent anomalies in the structure of northern fish populations began to appear in 1959, following a wide-ranging survey of the fishery potential of the lakes of the Barren Grounds (Johnson 1976). The Barren Grounds are that vast expanse of wilderness which stretches from the northern boundaries of the provinces of Manitoba, Saskatchewan, and Alberta to the Arctic Ocean. This region includes the world's greatest series of freshwater lakes, although even amongst limnologists, many of their names such as Angikuni, Kathawachaga, or Dubawnt are scarcely household words.

The fish populations in these lakes were found to be composed of large individuals, relatively uniform in size and generally of great age (Johnson 1976). When plotted, the length–frequency distributions of the dominant populations of lake whitefish (*Coregonus clupeaformis*) and lake trout (*Salvelinus namaycush*) resulted in bell-shaped curves indicating an almost total absence of small (young) fish. There was no indication in any of these plots of the expected negative exponential curve representing declining abundance as size and age increased. The pattern was universal so that one could either adopt the conventional view and accept the results as an artifact of the method of data collection (such as "gear selectivity"), shrug one's shoulders, or accept the burden of trying to develop a new approach.

The most effective and convenient sampling gear for isolated locations is the gill net, a fixed gear into which the fish swim in the normal course of their activity. Net selectivity is the assumption that nets function like a sieve so that small mesh sizes preferentially capture small fish and are generally of low efficiency whereas nets of large mesh size capture fish of relatively larger size.

The Barren Grounds Survey indicated that, although there were differences in the mean and modal length of fish captured in the various mesh sizes, the extreme difference between those from the largest mesh size (5.5 in. or 140 mm, stretched measure) and the smallest mesh size (1.5 in. or 38 mm) was very small (Fig. 1, 1959). This pattern was repeated in all lakes, although the actual modal values varied considerably among lakes. It did appear that the pooled sample from all mesh sizes provided a reasonable representation of the whole *active* population. No lake was observed in which the presence of a significant number of juveniles was indicated. This does not necessarily imply that there are no juveniles present, merely that they are not moving in the same space as the dominant segment of the population or "establishment".

The widespread occurrence of this pattern of age and size structure strongly indicated that the fish populations had reached a steady state. This was confirmed by repeated observations on some lakes at an interval of many years (Fig. 1, 1972).

Following the Barren Grounds Survey, experimental work was started at Keyhole Lake (Hunter 1970; Johnson 1983; Vanriel 1989) and detailed investigations begun on Great Bear Lake (Johnson 1975), Char Lake, Resolute Bay, Cornwallis Island (Schindler et al. 1974; Rigler 1975; Johnson 1983; MacCallum and Regier 1984), Nauyuk Lake (Johnson, 1980, 1983, 1989), and Borup Fiord lakes (Parker and Johnson 1991). Investigation of lakes in Greenland by

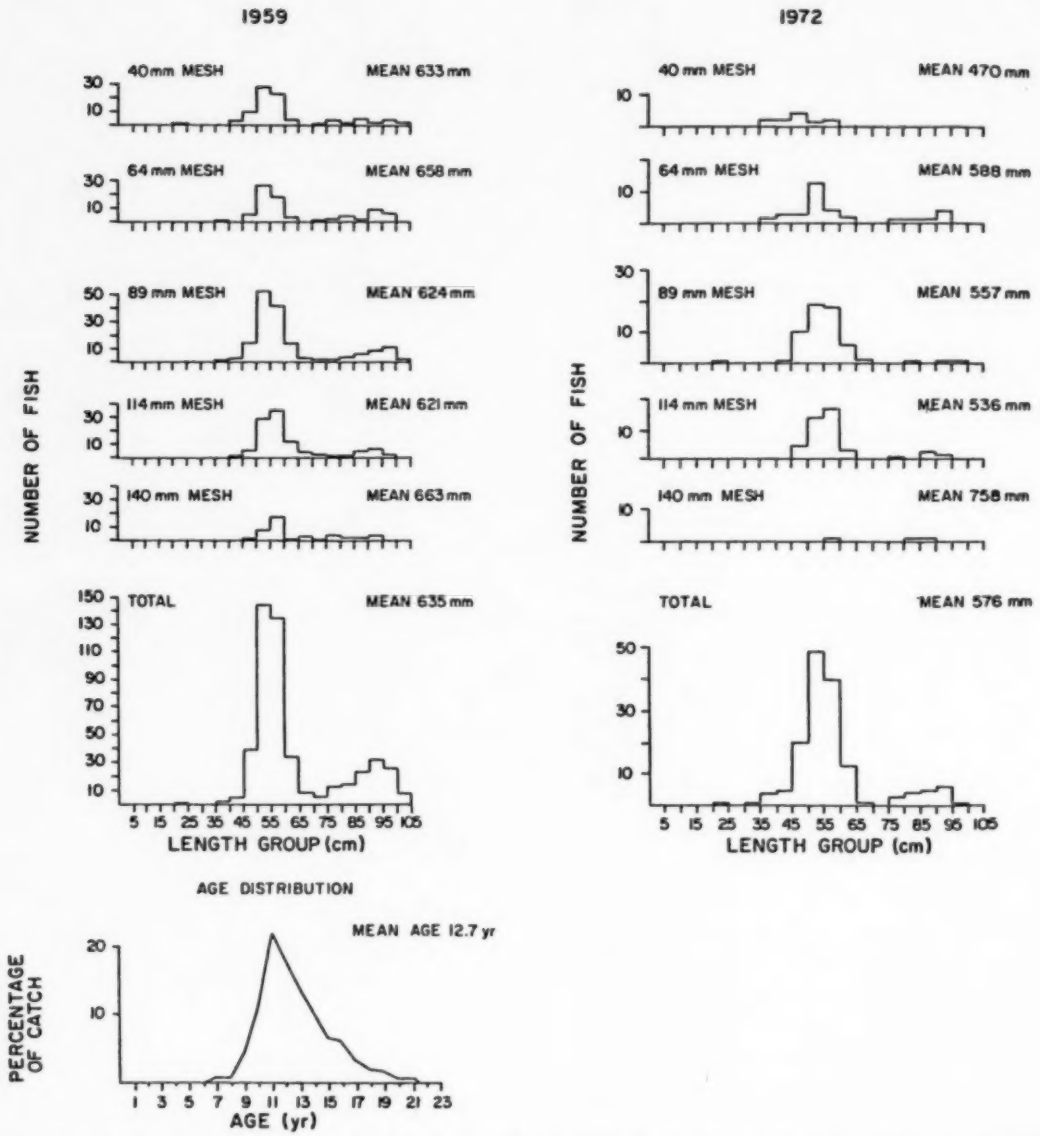


FIG. 1. Catches of (a) lake trout and (b) lake whitefish in 1959 and 1972, Lac La Martre, Northwest Territories, by mesh size. Essentially the same configuration is obtained in each year. (From Johnson 1976) (*Fig. 1 concluded next page*)

Sparholt (1985) and Riget et al. (1986) produced similar results. In a companion paper (Johnson 1994), I have detailed the findings from two small lakes, Gavia and Little Nauyuk lakes, that were studied over a 15-yr period. The results from these lakes confirmed the generality of the previous findings, although in these more detailed studies, juveniles were located along rocky shorelines using electrofishing techniques.

The population sample, whether Arctic char[2] (*Salvelinus alpinus*), lake trout, or lake whitefish, invariably exhibited a bell-shaped length–frequency distribution; in some cases, a second, smaller mode was evident, and in one case (lac La Martre), a larger, less numerous mode was evident. Within

[2]The author prefers "charr" rather than the American Fisheries Society spelling used as the editorial standard in this journal.

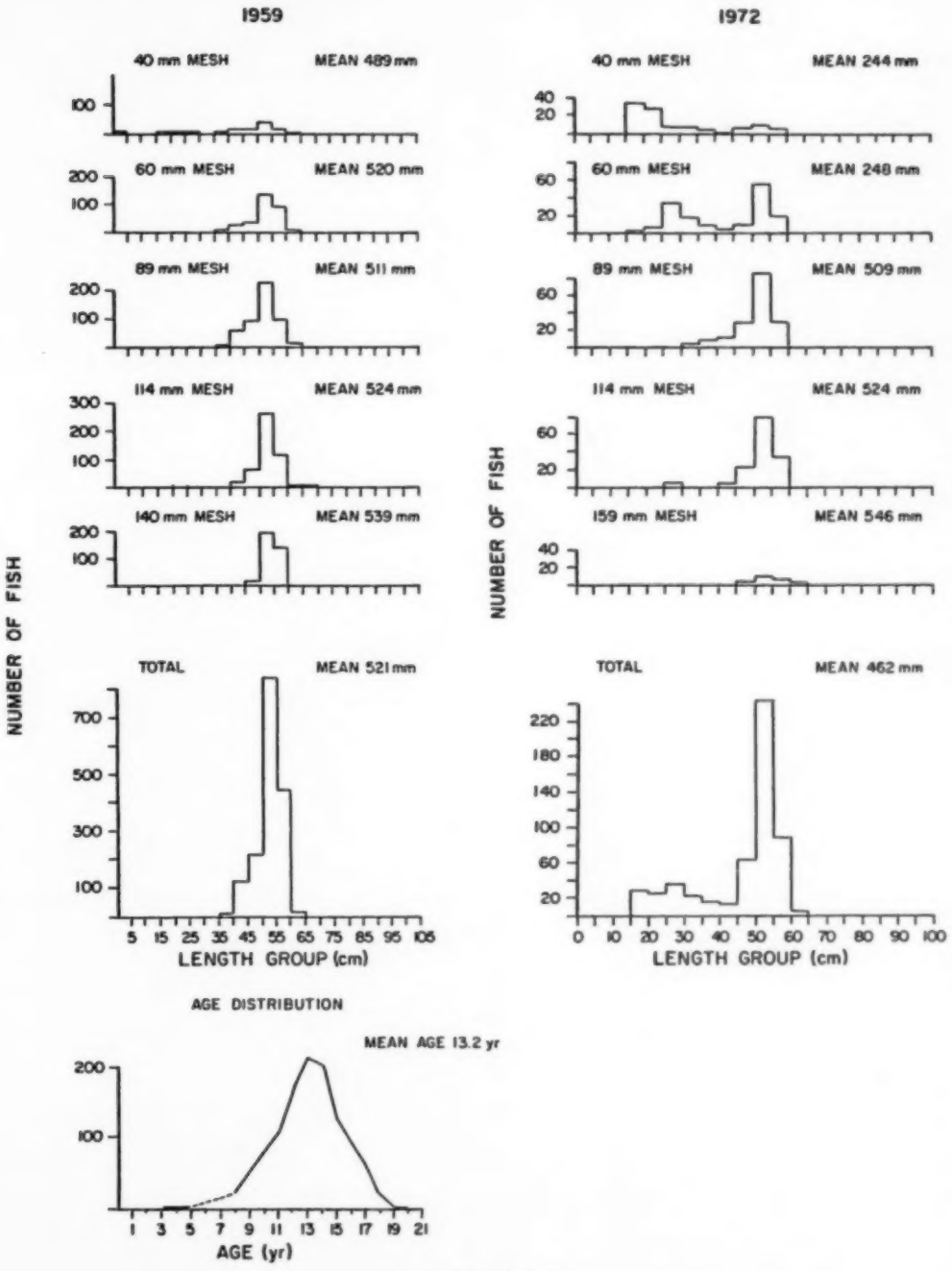


FIG. 1. (*Concluded*)

the major bell, each length class was composed of fish varying greatly in age, with the greatest range of age being found in the modal length class. There is quite a strong correlation between age and size, but given that size is a monotonic function of age, this might be expected. The bell-shaped length–frequency distribution is accounted for by

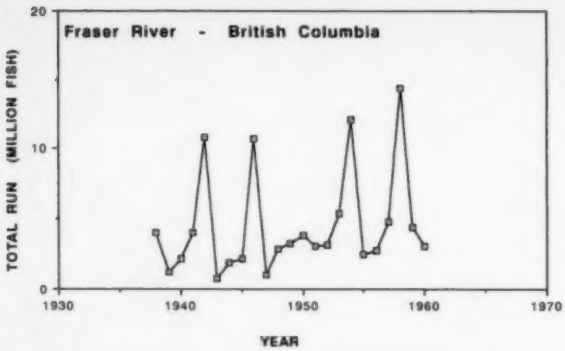


FIG. 2. Estimated total run of sockeye salmon from 1940 to 1960, Fraser River, British Columbia. (Data from Foerster 1968)

the wide dispersion of size within each age class. Such variability in the age of uniformly sized fish indicates that growth, as well as being under physiological control, is also partially regulated by interactions within the population. That regulation is not simply the result of density dependence was shown by the fact that populations maintained their structure as they declined in abundance under exploitation, as well as during the recovery phase when fishing operations ceased (Johnson 1983, 1994). The striking fact emerged that the population functioned as a cohesive unit, not merely as a collection of individuals.

From the generality and repeatability of the results, I reached the conclusion that arctic lake ecosystems are stable and this stability is, in large part, owing to a dominant fish species of large biomass and great age, maintained indefinitely through time by the gradual and ordered replacement of individuals (Johnson 1972, 1976, 1983, 1994). In the present context, stability means constancy in numerical abundance and in age and length structure, in the face of the environmental variability experienced over the recent history of the population (Johnson 1994). This stability provoked much thought, as it directly contradicted the diversity–stability hypothesis, which, when this work began over 30 yr ago, was very much in vogue (Elton 1924, 1958; MacArthur 1955; Kolata 1974; Johnson 1994).

The stable arctic lake system appeared to have strong structural affinities with the "climax" state of plant ecologists (Whittaker 1951, 1953; Johnson 1981). In this context, "climax" does not have any of the theoretical implications with which it has become imbued in vegetation theory (McIntosh 1985); it simply implies a relatively stable state, which may differ from place to place, depending on the incident species and local environment. The major structural difference between the arctic lake and, say, a mature forest is that the dominant species in a northern lake is terminal in the food chain whereas in the vegetational climax the dominant tree species is also the main primary producer.

The evident stability of northern lake fish populations was also in strong contrast with many intensively studied fish populations of temperate climates where fluctuations are considered to be an inherent characteristic. Since biblical times, the history of commercial fisheries indicates that there are good years and bad. In addition to St. Peter's experience, certain fisheries have been recognized as being particularly subject to regular fluctuation. Since the start of the commercial fishery for sockeye salmon (*Oncorhynchus nerka*) on the Pacific Coast, and long before the intensity of exploitation could have significantly affected stocks, catches varied greatly from year to year (Fig. 2). According to Foerster (1968, p. 55):

> One authority [Semko 1953] reports that: 'After 50 to 60 years' experience in the salmon fisheries we know that sharp fluctuations in the size of the salmon runs occurred not only at the very start of the industry, when exploitation was extremely light, but also later during the years of a highly developed fishery. This suggests that intensity of exploitation is not the major factor determining the condition and annual variation in the salmon stocks'

Thus, it must be accepted that some fish stocks fluctuate whereas others exhibit a high degree of stability; furthermore, these differing stocks may be quite closely related, even belonging to the same family. Similarly, in botanical theory the relatively long-term stability of forests may be contrasted with the cyclic vegetational patterns in sphagnum bogs discussed by Watt (1947).

Strong Inferences

The first inference from these observations was that the prime reason for stability in lake systems was their high degree of autonomy. As Tansley (1935) observed: "The more relatively separate and autonomous the system, the greater the stability of its dynamic equilibrium." The second was that the physical properties of water buffer the highly variable terrestrial climate, thus providing a relatively uniform, even if extremely lean, environment.

Are Arctic Lake Ecosystems Unique?

The next question to be answered was: is the configuration of the arctic lake ecosystem unique, owing to some unknown property of "arcticness", or is a general biological principle involved? As the latter seemed to be the more believable approach, a search was made for similar situations in all parts of the world. In the event, a number of meticulous studies were found, usually in interesting corners of the world where man's previous influence had been negligible, or had had sufficient time to be obliterated.

White Sucker (*Catostomus commersoni*) of Heming Lake, Northern Manitoba

Heming Lake lies in the boreal forest in latitude 55°N. Under the direction of Dr. G.H. Lawler of the Freshwater Institute, an extremely interesting and complex data set was collected extending over 18 yr, from 1952 to 1970. The work at Heming Lake was designed primarily to determine whether cysts of the parasite *Trienophorus* spp. could be eliminated from the flesh of lake whitefish by reducing the population of northern pike (*Esox lucius*), the final host of the parasite (Lawler and Watson 1958). The research program called for continuous monitoring of all fish populations and limnological parameters in addition to the concerted attempt to reduce the pike population. The data on the white sucker population (Fig. 3) emerged out of the monitoring program.

In 1952, white sucker exhibited a bimodal length–frequency distribution, and then, as fishing intensity increased,

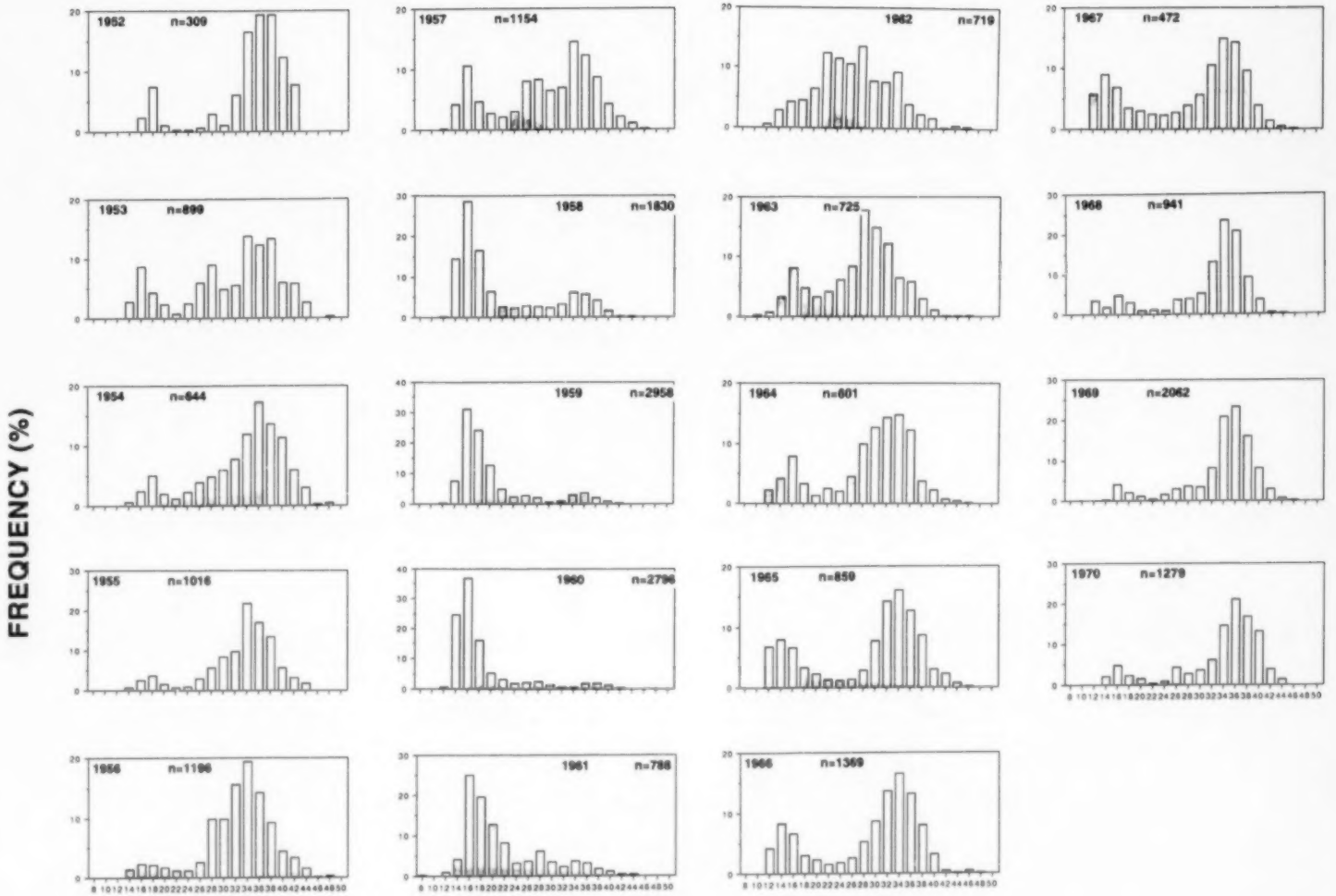


FIG. 3. Length–frequency distribution of white sucker between 1952 and 1970, Heming Lake (53°N), Manitoba. (Data courtesy of G.H. Lawler and J.S. Campbell)

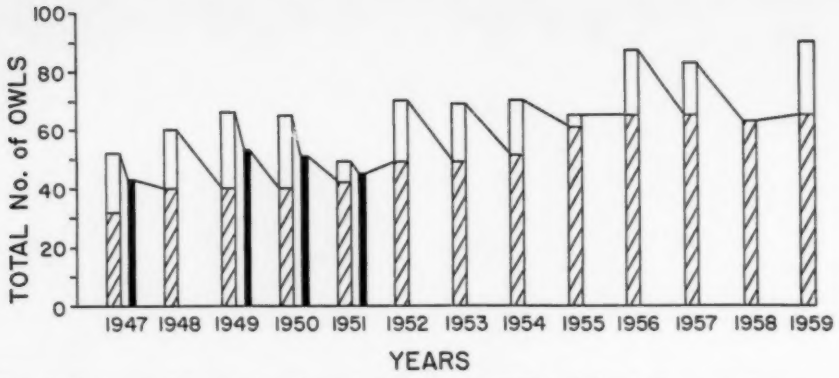


FIG. 4. Recovery of the tawny owl population following 50% depletion in the unusually severe winter of 1947, Wytham Woods, Oxford, England. The number of territory-holding owls is indicated by the hatched region and the fledglings by the open areas; narrow black columns indicate an autumn census. (Redrawn from Southern 1970b)

the relative abundance of the larger mode declined, while that of the smaller one increased; eventually, after 10 yr fishing, the large mode had been virtually eliminated. When the fishing pressure was reduced after 1961 the large mode began to reform in a very coherent manner. A group of recruits moved in a phalanx through the size classes until the original configuration was regained. Only in 1962 was there any appreciable fraction of the population in the size classes forming the "trough" between the two original modes. Physicists might state that, for stability, there are only two "allowable" size groups. However, unlike an electron moving from a higher to a lower energy state in its shell around the atomic nucleus, we do get, in 1962, a glimpse of the transitional state. These data demonstrate the highly cohesive and well-organized nature of the white sucker population in a remarkable and unequivocal way.

Tawny Owls (*Strix aluco*) in Wytham Woods, England

Similar coherence was manifested by the tawny owls of Wytham Woods, Oxford, studied in great detail by Southern (1970a, 1970b). Wytham Woods is a relatively isolated block of woodland set in the midst of farmland. An unusually severe winter in England in 1947 caused the death of nearly half the adult owl population. Over the next 10 yr, there was a monotonic increase in number as the population gradually returned to its original level of abundance. After 1947 the remaining owls expanded their individual territories to include the whole available area; then, only gradually, was each territory reduced in size as, each year, a small number of recruits gained access to additional territories. The rate of increase did not appear to be affected by either the food supply or the number of potential recruits (Fig. 4). Potential recruits, unable to secure a territory in Wytham Woods, presumably left the area to search elsewhere, for marked juveniles were occasionally found dead of starvation outside the research area. Finally, a density was reached at which territories could be completely defended and a relatively stable state reestablished. Thus, although the population at the stable state may be density controlled, recruitment at levels below this ceiling is regulated by cohesion within the "establishment". Fluctuation in abundance during the recovery process is thereby effectively damped.

European Virgin Forests

Jones (1945) surveyed the remnants of European virgin forest. While he believed that little if any of the forest still existed entirely free from the effects of fire, grazing, or other human impact, the structure of the dominant tree species showed strong modal tendencies. Describing a particularly uniform stand of beech (*Fagus sylvatica*) in a Bosnian forest, Jones stated:

> Regeneration in such forests often appears to be absent, and there is a striking deficiency of smaller stems, giving a diameter distribution which may approach that of an even-aged stand. This, however, does not mean that the forest is not reproducing itself and maintaining the present structure.

Similar observations have been made by Morey (1936a, 1936b) in North American forests. In one example, Morey found that the age of hemlock (*Tsuga canadensis*) in the hemlock consociation changed directly as the diameter at breast height (dbh), but in only two thirds of the cases did the age fall within ±42.7 yr of the estimate. For example, a hemlock of 32 in. (81 cm) dbh would, in two cases out of three, be between 359 and 445 yr of age. Thus, large size, uniformity in size, a very variable age at modal size, and an apparent dearth of juveniles appear to be general characteristics of the climax forest of Europe and North America.

Giant Land Tortoises (*Geochelone gigantaeus*) on Aldabra Atoll, Indian Ocean

Aldabra Atoll tortoise populations were examined intensively over a number of years (Gaymer 1968; Grubb 1971; Gibson and Hamilton 1983 and references therein). These studies resulted from the planned construction there of a British military air staging base, although, with the advent of long-range jet aircraft, the project was later cancelled.

In the mid-nineteenth century the tortoise population was heavily exploited for the "tortoise shell" trade and reduced to near-extinction. As early as 1874, a letter to the governor of Mauritius (the responsible authority for the Atoll) signed by, among others, Charles Darwin, Richard Owen, and Joseph Hooker expressed concern over the imminent extinction of the tortoises. The Atoll was given protection in the

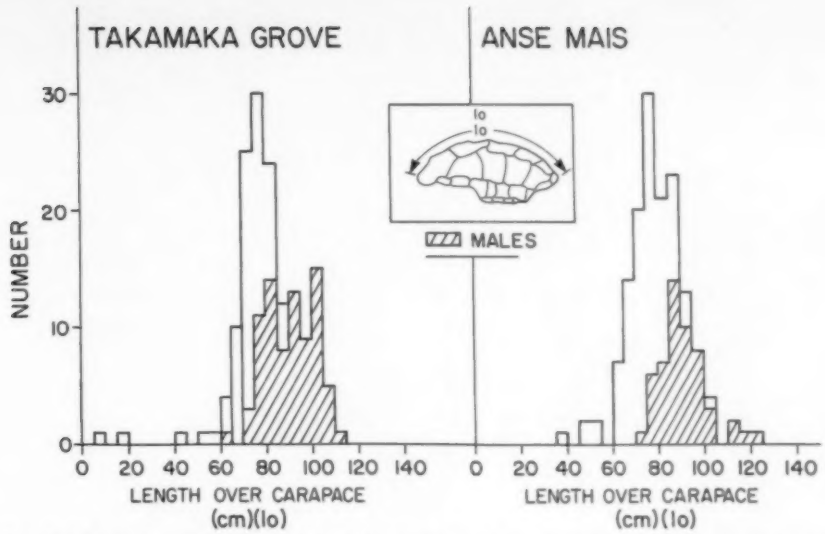


FIG. 5. Length–frequency distribution of giant land tortoises at two locations in the Aldabra Atoll, Indian Ocean: Takamaka Grove and Anse Mais. (Redrawn from Gaymer 1968)

early part of this century and eventually became a reserve under the auspices of the British Royal Society. The tortoises recovered and today appear to be flourishing, although in some populations there is evidence of very low rates of replacement and even population decline (Bourn and Coe 1978).

The giant tortoise in Aldabra is believed to be the only known case of a reptilian population occupying the dominant role in an ecosystem (Bourn and Coe 1978). Tortoise size reaches 100 cm in carapace length, and ages up to 60 yr were estimated to be quite common (Fig. 5 and 6). Age–frequency peaks at 13–14 yr of age, although beyond this age the difficulty of accurate assessment increases (Grubb 1971). The low number of juveniles cannot be attributed to gear selectivity, as the tortoise spends the whole of its life cycle on land. When juveniles were specifically sought, relatively few were found and when found, they were occupying a different habitat from that of the adults, living mainly in cracks and fissures in the rocks, inaccessible to large animals. These studies echo those on northern fish populations; for example, the length–frequency distributions of lake trout from Great Bear Lake and tortoises from Aldabra are virtually indistinguishable in the absence of appropriate legends (Fig. 7).

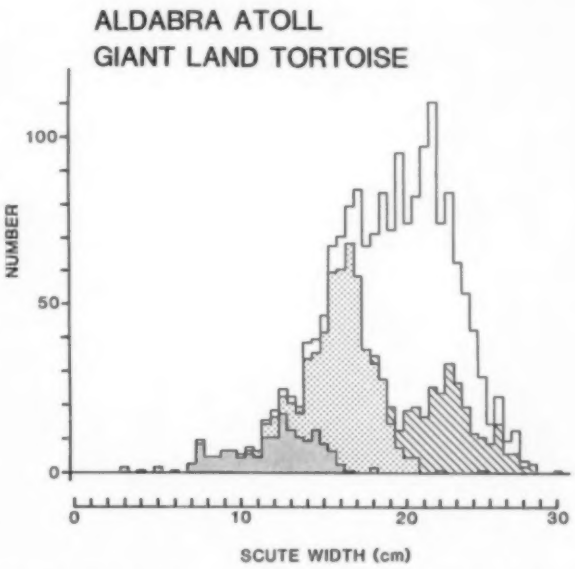


FIG. 6. Giant land tortoises showing size and age distribution, Aldabra Atoll, Indian Ocean. Overall size was correlated with the length of the third scute in 1771 tortoises examined. Four categories are distinguished: tortoises up to 10 yr old (heavy stipple), tortoises 11–20 yr old (light stipple), adult unaged males (hatched), and males + females, unaged (open). (Redrawn from Grubb 1971)

Swan Mussel (*Anodonta grandis*) in Aeroplane Lake, Inuvik, N.W.T.

Green (1980) studied the calcium metabolism of swan mussel in a small arctic lake in the Mackenzie Delta. Sampling the mussel population was done by divers sieving the sediments. Ages were estimated by counting annuli deposited in the shell. No specimens under 5 yr of age or less than 50 mm in length could be found (Fig. 8). The generality of this situation was shown by similar length–frequency distributions of the freshwater mussel *A. grandis grandis* in lakes of the Precambrian Shield (Malley et al. 1989; Huebner et al. 1990). The general absence of juveniles does not appear to indicate impending local elimination of the population, as Wieser et al. (1981) suggested was the case for a similarly structured snail population (*Batillaria minima*) on a Bermudan sand-flat, nor can the existence of a sampling artifact be assumed. It simply means, mystifying though it may be at present, that we need more information before we can comment on the actual recruitment mechanism involved.

Nile Perch in Lake Tanganyika

Three species of Nile perch, *Lates mariae*, *L. microlepis*, and *L. angustifrons*, and one of the close relative *Luciolates stappersii* inhabit the pelagic region of Lake Tanganyika above the permanently anoxic deep water (>100–200 m) A closely monitored purse-seine fishery on these species was inaugurated in 1958 and the studies were backed up by detailed limnological observations (Coulter 1963, 1970, 1976). Coulter showed that the pelagic populations were strongly unimodal in their preexploitation configuration (Fig. 9). Juveniles (<20 cm in length) were captured only in weedy areas near shore. After several years of intensive fishing of the *Lates* stocks, there was a considerable reduction in abundance but little change in modal size was observed. Ages, as in most tropical fish, were difficult to determine precisely, but the fish were estimated to reach the asymptotic size of 60 cm at 7 yr of age.

Regenerating Forests in Michigan

In controlled plots in northern lower Michigan, Sakai and Sulak (1985) recorded the changing structure of the regenerating forest following clear-cutting. A negative logarithmic distribution of saplings in the early years gradually gave way, over the course of about 40 yr (Fig. 10), to a unimodal size distribution in the maturing forest. This case is of particular interest because three species functioned in concert to achieve the final distribution.

Orange Roughy (*Hoplostethus atlanticus*) in the Deep Seas

The orange roughy has worldwide distribution in deep waters where it occurs in great abundance. Detailed studies on populations in deep waters (400 m) off the coast of New Zealand were carried out by Gauldie et al. (1989). Gauldie and his co-workers pointed out strong similarities in age and size characteristics between the orange roughy and Arctic char and how, when heavily exploited, the populations, similarly, retained their initial modal structure (Fig. 11).

Giant Clams (*Tridacna maxima*) of Rose Atoll, American Samoa

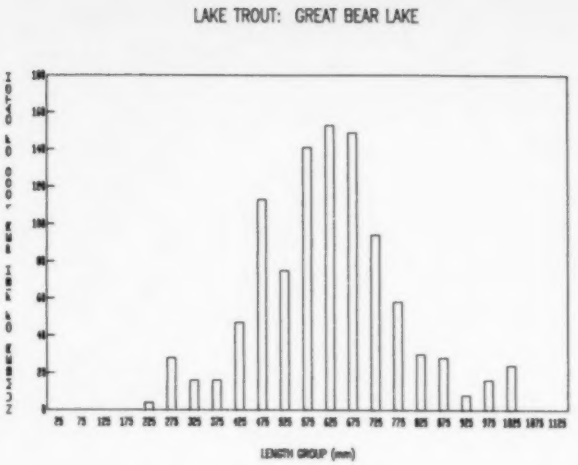
A strongly bimodal structure was observed, with small clams occupying the deeper waters and larger ones the shallower regions of the lagoon (Radtke 1985) (Fig. 12). Radtke estimated the average age of a clam with a 200-mm shell length to be about 18 yr.

Dinosaurs in Montana

A remarkable find on the Willow Creek Anticline in Montana was an enormous bed containing the fossilized bones of at least 10 000 individual maiasaurs. According to Horner and Weishempel (1989):

> Members of a huge herd they were apparently killed simultaneously in a great volcanic explosion and were entombed in the ashes. Because they all died at the "instant" of catastrophe, their size distribution represents the standing age distribution of the living herd. Most individuals were from twelve to twenty-five feet in length, something like the maiasaur version of the teenage years and older. Young maiasaurs are missing.

In the same general vicinity, nesting sites (containing



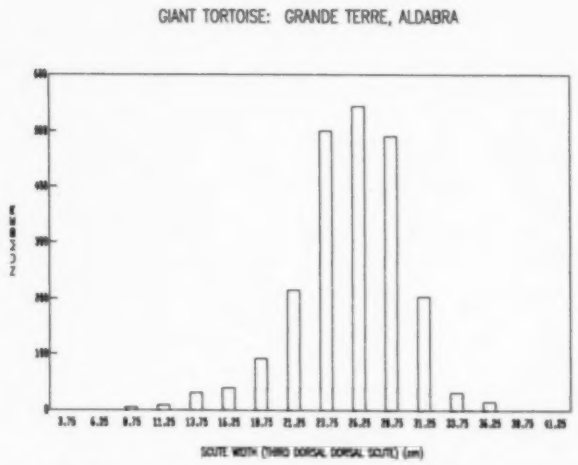


FIG. 7. Comparative size distributions of Great Bear lake trout and Aldabra Atoll giant land tortoises from Grade Terre.

remarkably well-preserved dinosaur eggs and embryos) were found, so that there seems little doubt that the population was maintaining itself.

Other examples were found, such as the blind cavefish (*Caecobarbus geertsii*) of Zaire (Heuts 1951), which is the only ecosystem that, to my knowledge, consists of but a single species. The fish live in complete darkness, feeding on detritus carried into the caves during the wet season. In only one of the many caves Heuts examined did he find juveniles, and then in anomalous conditions near the cave entrance. Similarly, the blind cavefish of the southern United States (northern cavefish (*Amblyopsis spelaea*) and Ozark cavefish (*A. rosae*)) (Poulson 1963) also showed a virtual absence of young fish, although the "missing" age groups invariably appeared as adults in subsequent years. Comparable population structures were found in the reef fishes of northeastern New Zealand (McCormick 1989).

Mammalian herds on the world's grasslands can be assumed to have had a similar size/age configuration to those of an arctic fish population, although in such cases, size

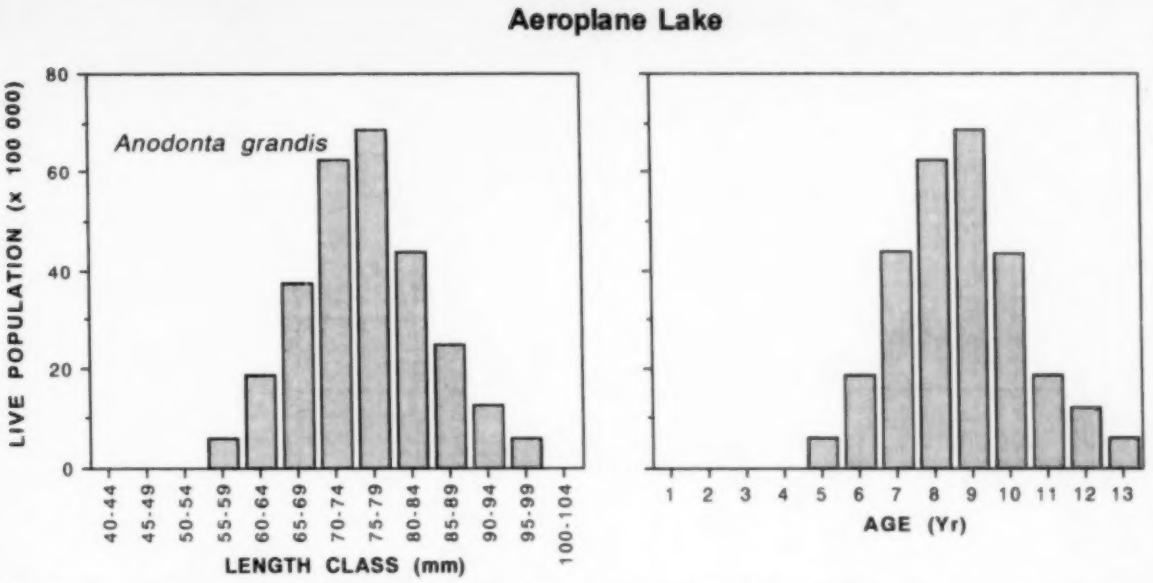


FIG. 8. Size– and age–frequency distributions of swan mussel, Aeroplane Lake, Inuvik, N.W.T. (Redrawn from Green 1980)

being regulated genetically, this type of structure might be expected. However, this is not the case with fish or trees which have an indeterminant growth pattern. If, as may be presumed, a determinant growth pattern evolved from an indeterminant one, then size uniformity has survival value.

From these examples, it is evident that the dominant populations in autonomous ecosystems in all parts of the world exhibit similar configurations.

Origin of the Observed Pattern

The initial premise I adopted, when attempting to distil process from the basic pattern, was that living organisms, being a composite of energy and materials and dependent for their existence on exploiting the energy gradient between the sun and the universe, obey recognized principles of physics. The energy gradient is created by the assimilation of short-wave energy of low entropy, with a capacity to do work (free energy in Helmholtz's formulation) and its subsequent degradation over time, until, when it can perform no further work, it is discharged as long-wave radiation (heat).

Ever since the principles of energy flow and distribution gradually emerged in the nineteenth century, there have been attempts to unify the basic concepts of physical and biological systems. Nevertheless, thermodynamics has not been popular amongst biologists (Hull 1988): for example, a recent collection of papers on theoretical ecology (Roughgarden et al. 1989) does not even mention thermodynamics. This, I believe, is owing to the difficulty of reconciling a limited range of biological observations with a rather narrow interpretation of thermodynamic laws.

Despite this general lack of enthusiasm, interest in the physical basis of living systems has been intense among a relatively small number of workers (Lotka 1924, 1945; Lindeman 1942; Prigogine and Wiame 1946; Odum and Pinkerton 1955; Kirkaldy 1965; Trincher 1965a, 1965b; Morowitz 1968; Odum 1969; Odum 1971, 1988; Ulanowicz 1972, 1986, 1989; Hannon 1973, 1979; Prigogine 1978; Jørgensen and Mejer 1979, 1981; Wicken 1980, 1987, 1989; Jantsch 1981; Johnson 1981, 1988, 1990, 1992; Bernstein et al. 1983; Hirata and Ulanowicz 1984; Kay 1984, 1991; Brooks and Wiley 1988; Weber et al. 1988, 1989; Depew and Weber 1989; Swenson 1989; Kay and Schneider 1992; Månnson and McGlade 1993; Patten 1993). Weigert (1988) discussed the history and the present and future prospects of ecological energetics.

A warning by Kirkaldy (1965) that "...quantitive advances can only cloud the issue in an area where qualitative answers must first be sought" is, I believe, too often ignored. Patten (1993) made a comparable plea to understand H.T. Odum's work in a relatively relaxed framework rather than judging it by the harsh light of mathematical thermodynamics. The following hypothesis is also largely qualitative but written in the belief that a more rigorous thermodynamic treatment is possible and will follow in due course.

The Reference System

In classical thermodynamics the reference system is an imaginary "isolated" system which exchanges neither energy nor entropy with the external world; in such a system the entropy assumes a maximum value. A "closed" system is one in which free energy impinges on the system, is time-delayed, then gradually degraded through work processes, until finally dissipated to the external world as long-wave radiation. There is no exchange of materials with the external world. An "open" system is one in which both energy and materials are exchanged with the external world.

Ecosystems are generally considered to be open systems, although at the highest level the whole biosystem of the earth functions as a single "closed" system in which ecosystems are subsystems, partially bounded by biological and physical factors. The biological boundaries of a specific ecosystem gradually expand while physical boundaries fluc-

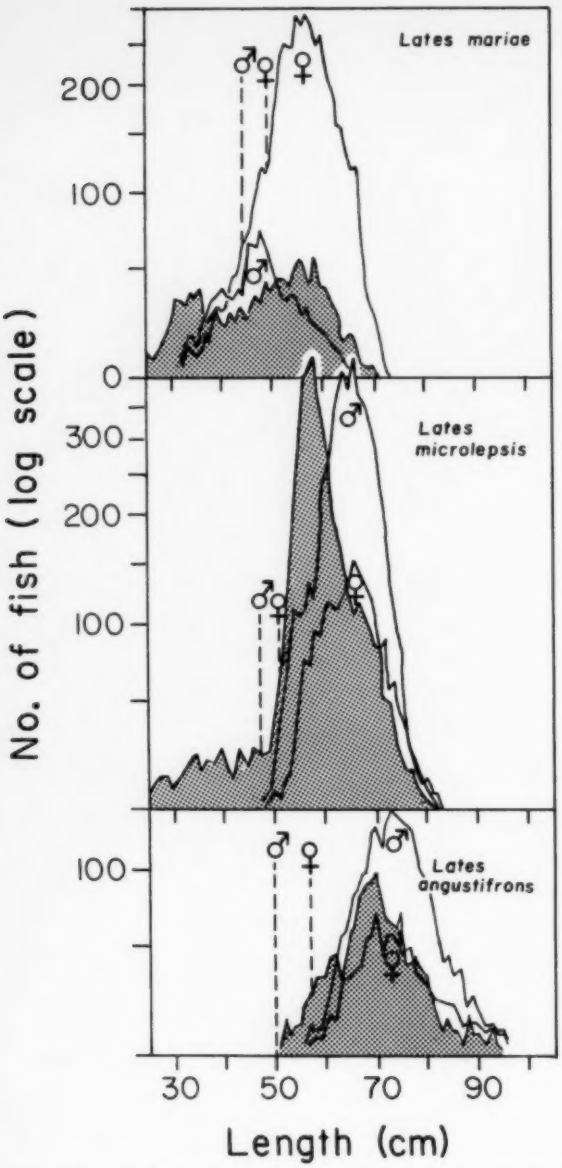


FIG. 9. Length–frequency distributions of *L. mariae*, *L. microlepis*, and *L. angustifrons* showing initial distributions and distributions after heavy fishing, Lake Tanganyika, East Africa. 1962–63, open (males and females separately); 1967–68, stippled (males + females). (Redrawn from Coulter 1970)

tuate, until, at the uppermost level, all ecosystems are constrained by the biosphere boundaries. Such constraints will have been most significant when the biosystem is in a relatively steady state, such as evidently occurred during the long periods of evolutionary stasis between periods of rapid change (Gould and Eldredge 1977). During periods of rapid change, such as are occurring at present, constraints are greatly lessened, which allows certain elements of the system to "run wild" until they meet new boundaries.

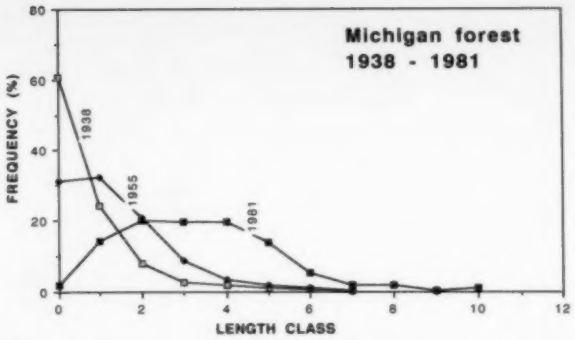


FIG. 10. Changes in the pooled size class distributions of three species of conifer, northern white cedar (*Thuja occidentalis*), black spruce (*Abies mariana*), and balsam fir (*Abies balsamea*) in lowland northern Michigan forests. (Redrawn from Sakai and Sulak 1985)

A biological reference system is envisaged as a completely autonomous or closed ecosystem, experiencing a regular input cycle of free energy from the sun (or other source), but experiencing no exchange of materials or matter with the external world, all materials being completely recycled. If we can establish the pattern of energy distribution within such a system, we should gain great insight into ecosystem thermodynamics.

The Real World

The conditions in a small arctic lake closely approach those of the imaginary reference system (Vanriel 1989). At the same time, they meet the conditions regarded as the most propitious for the initiation of a study on complex systems (Platt 1964): start with the simplest system available which contains all the parameters of interest.

For 9–10 mo of the year, an arctic lake, encapsulated beneath a thick layer of ice, and having neither inflow nor outflow of materials, functions as a completely "closed" system. As soon as the sun returns in late winter, light penetrates the ice and photosynthesis begins (Welch and Kalff 1974). Break-up occurs in late June – July, and for 2–3 mo of open water, there is a limited exchange of both energy and materials with the outside world mainly through predation by birds and insect emergence. However, this is not considered sufficient to affect significantly the general ecosystem structure.

The general characteristics of the autonomous populations described above are high biomass, large, relatively uniform size, considerable mean age, very few juveniles (sometimes none evident), variable age at a specific size (with greatest variation in age occurring within the modal length class), a variable age at death resulting in desynchronization of the life cycle, and maintenance of this configuration indefinitely over time. Following severe disturbance, such populations revert to their original configuration without significant oscillation.

Least Dissipation

Together, these characteristics define a state of "least specific dissipation" (or "least entropy production") which is the rate of energy dissipation relative to unit biomass or,

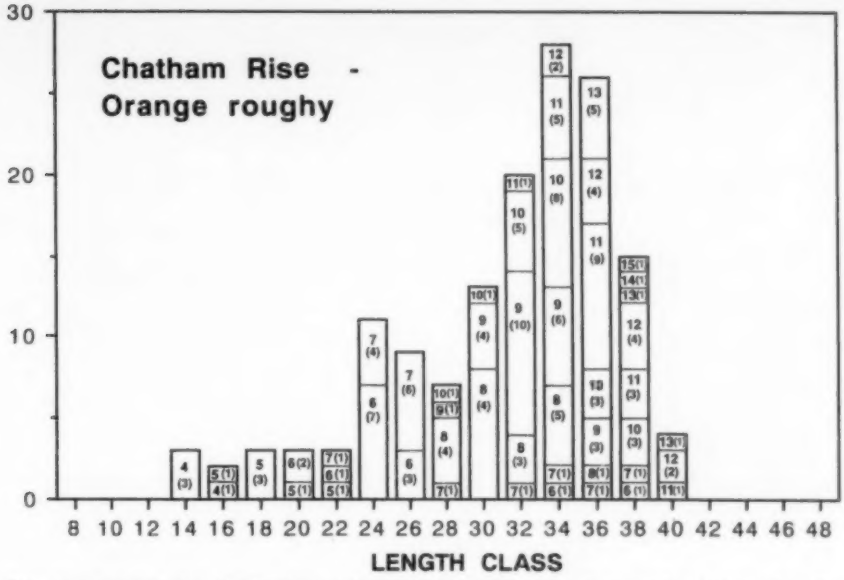


FIG. 11. Age and size distribution of the orange roughly in the deep marine waters of northern New Zealand. (Redrawn from Gauldie et al. 1989)

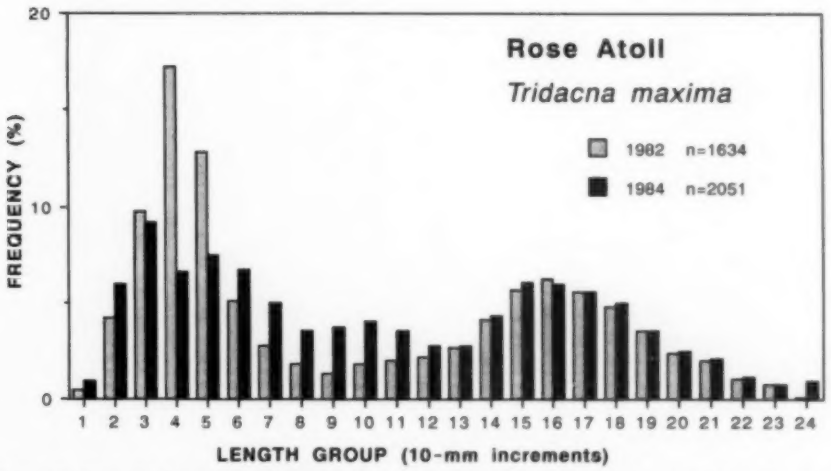


FIG. 12. Length–frequency distribution of the giant clam, Rose Atoll, American Samoa. (Redrawn from Radtke 1985)

alternatively, to biomass per unit area. Least dissipation is the least "attainable" in the prevailing environmental conditions, the associated species, and the genetic make-up of the population. Thus, the larger the individual size (the larger the size, the lower the specific metabolic rate (Kleiber 1961)), the greater the mean age (the longer the turnover time), and the greater the continuity, the less the overall rate of dissipation.

Prigogine (1978) stated:

> According to the theorem of least *S* [entropy] production, the *S* production is...a Lyapunov function in the strictly linear region around equilibrium. If the system is perturbed, the *S* production will increase but the system reacts by coming back to the minimum value of the *S* production.

Clearly, Arctic char in a small autonomous lake obey the theorem of least dissipation. If the population is exploited, the rate of dissipation increases as life spans are prematurely terminated. When the perturbation ceases, this characteristic provides a damping mechanism that ensures that the population reverts to its original state without significant oscillation (Johnson 1983, 1994). The system thus continuously seeks a state of least dissipation, despite perturbations caused by inevitable variation in the environment.

"Least dissipation" may be said to function as an "attractor" state for all other states. The "attractor" is a state of zero dissipation or complete stability (as in the formation of a crystal), but this, of course, is a lethal state for an organism. An organism may therefore be regarded as existing in a condition analogous to incipient crystallization.

A single reference system such as an arctic lake does not cover all ecological situations. An arctic lake has a more or less linear food chain in which energy passes from the primary producer, through a detrital loop, to the terminal heterotroph which is also the dominant species (Vanriel 1989). Conversely, in a forest system, the roles of principal primary producer and dominant species are played simultaneously by the same actor. Food chains in a forest develop secondarily by organisms feeding on the leaves or flowers of the dominant species and on subordinate plant species. Thus, there appear to be at least two basic reference systems necessary: one in which the dominant species is the terminal predator and the other in which it is the primary producer. A forested oceanic island, prior to its invasion by man, might serve as a conceptual reference system for one dominated by its primary producer.

A third widespread ecological type, the grassland, is similar in essentials to the lake system: energy in the leafy part of the grass passes directly to the terminal herbivore and there accumulates in vast herds of ungulates, marsupials (in Australia), or birds (moas, now extinct, in New Zealand). Again, as in the lake, the major energy reserves in grasslands are found in the humus developed from decaying roots and surface litter (Dyksterhuis and Schmutz 1947; Ryszkowski 1975). Predators on the dominant animal species certainly exist, but appear to exercise little control on the ultimate abundance of their prey. Thus, although the dominant species may vary with respect to class and even phylum, it always exhibits the basic characteristics of large individual size, high biomass, great age, and a low incidence of juveniles.

Dominance and Succession

Dominance

"Dominance, in fact," Whittaker (1957) stated "is one of the master-keys to the understanding of vegetation, as successional process is another." Similarly, it seems, it is the key to understanding animal communities. According to McNaughton and Wolf (1970), dominance is a characteristic of the most abundant species and it is the species with a broader niche than subordinate species. The dominant species is the one which is least controlled in its abundance by other species, being largely constrained by the physical boundaries of the ecosystem, its food supply, and its genetic constitution. In plant associations the dominant species controls the energy input and the energy available to other components of the ecosystem. That is, it exerts both "bottom-up" and a "top-down" control on the ecosystem. The dominant species in aquatic and grassland systems exerts only a "top-down" constraint on other organisms present (Northcote 1988) but, at the same time, stimulates turnover rates in subordinate species.

Succession

Succession is the complex process whereby a relatively steady state is reached from a changing state caused by changes in either the physical or biological environment. According to Clements (1905, p. 266):

> The number of species is small in the initial [successional] stages, it attains a maximum in intermediate stages and then decreases in the ultimate formation, on account of the dominance of a few species.

Similarly, Tansley (1923, p. 127) stated:

> The later stages of development are often marked by an actual decrease in the number of species, since many of those existing in the middle stages of development...are unable to subsist under the ultimate more extreme and uniform conditions.

A reduction in species richness can be seen also in neighbouring small arctic lakes, which vary considerably in their present species complex, although all having had the same initial complement at the time when they emerged from beneath the ocean (Johnson 1980). This general process was discussed by Whittaker (1969 and references therein) and recognized by Odum (1969).

An increase in the biomass of the dominant species relative to that of the rest of the system reflects the decline in the production to biomass ratio (P/B) as the system matures (Margalef 1968). Thus the system as a whole as well as the dominant species tends toward "least dissipation".

Dominant species have been observed to occur in many phyla and classes in various parts of the world; therefore, one may conclude that the general trend to "least dissipation" is not confined to the dominant species; in fact, all species are assumed to tend toward a state of "least dissipation", but in species other than the dominant, the full manifestation of such as state is prevented by interspecific interaction. It seems that there are no specific genes for dominance: each species pursues a path according to its inherent characteristics, carving out for itself the "best" position that it can. It is evident also that a rigid trend to "least dissipation" is not universal among species. Some, such as the Pacific salmon, in pursuit of their own "best interests" but within the constraints experienced, develop a determinant life cycle inducing fluctuations, apparently contrary to a state of least dissipation.

If the thesis is accepted, that the dominant population in an autonomous ecosystem assumes a state of dissipation and that the system as a whole tends also to a state of least dissipation, then the rest of the argument develops logically on the basis of established thermodynamic principles.

Ecosystem Thermodynamics

It is postulated that an ecosystem is structured on the outcome of two nearly equal but opposing forces, one tending to delay energy passage through the system and the other tending to accelerate it. Over successional time, the system is dominated by the trend to "least dissipation" whereas over evolutionary time, the dissipation rate tends to increase.

The origin of these two opposing forces appears to lie at the most fundamental level. When a photon is captured by an atom, the atom is raised to a higher energetic state as an electron in the shell around the nucleus is lifted to a wider orbit; there is then a time lag of 10^{-7}–10^{-8} s before the atom returns to its ground state with the discharge of a photon (Szent-Gyorgi 1961). A cyclic energy pathway of very brief duration was thus established in a suitable substrate when exposed to sunlight. Through resonance, as energy was stored the time-delay tended to increase.

This cyclic energy pathway interferes with the normal rectilinear propagation of radiant energy. Onsager's (1931)

reciprocal relations stipulate that when two energy transport processes interfere with each other and the energy is conserved, the system goes to a state of least dissipation. The theorem of least dissipation applies, strictly, only in the vicinity of thermodynamic equilibrium where the relationship between forces and flows is linear.

It is therefore hypothesized that the protobiological system originated as a resonant response to intermittent sunlight in a chemical "broth" existing in a state close to thermodynamic equilibrium. The uniform energy-charged "symbols" (proto-organisms) thus created functioned as a *tabula rasa* capable of identifying an array of environmental signals (Polanyi 1968; Scheer 1970).

Living entities are believed to have originated close to thermodynamic equilibrium through interference between cyclic and rectilinear energy transport processes. Atoms and molecules, being more reactive at higher energy levels, formed compounds which existed through the performance of work for as long as the higher energy state lasted. The tendency to "least dissipation" resulted in an increase in the time delay, causing the energy in the photon to be dissipated more slowly, thereby increasing its work potential. This is owing to the fact that the slower that work is done, the greater the efficiency with which it is performed (Odum and Pinkerton 1955; Gnaiger 1983, 1986). Gradually, the system evolved away from near thermodynamic equilibrium under the influence of the two opposing forces acting in different time frames.

The work potential thus created materialized in "dissipative structures". "Dissipative structures" are ordered structures in the energy flow (Neumann 1978):

> Such flow structures exist only within certain boundary conditions and survive only on energy input dissipated in the maintenance of the flow pattern. Dissipative structures have been recognized to exist only far from equilibrium where the relationships between flows and forces are non-linear.

Prigogine (1978) maintained that dissipative structures, established in physical or chemical systems, far from (thermodynamic) equilibrium, do not obey the theorem of least dissipation, although in his earlier publications (Prigogine and Wiame 1946), he did believe that this was the case in organisms. Nevertheless, it is evident that biological entities, which certainly fall within the definition of dissipative structures, exist far from thermodynamic equilibrium, yet do assume a state of least dissipation when allowed to proceed to an "end-point".

This apparent conflict can be resolved by postulating that the forces, initially manifesting themselves only in the vicinity of thermodynamic equilibrium, are amplified through an increase in energy input, and an increase in its time delay, but continually constrained by the opposing trend to increase the dissipation rate. As the system is open to change, it gradually moves away from thermodynamic equilibrium *provided the amplified forces maintain a nearly symmetrical (equal and opposite) condition.*

Action Principles

The "principle of least action" is universal in its application in physics, although to the best of my knowledge, it has not previously been applied to living things. Zee (1986, p. 109) stated: "All physical theories established since Newton may be formulated in terms of an action." "Action" is the product of *energy* and *time* and is measured in joule-seconds in the International System of Units. The importance of time as a dimension in biology, rather than indicating the general direction of events, as provided by the Second Law, is evident in the limited but variable life span of most species. Moreover, the application of "action" concepts fits the events of the real world more closely than does that of "dissipation".

The principle of least action was originally developed as a mechanical equivalent of Fermat's principle of least time. Pierre de Fermat, the great French mathematician of the seventeenth century, found that a ray of light passing through transparent media of different refractive indices takes the path of "least time", which is not necessarily the shortest path (Feynman 1963; Watson 1986). It is therefore postulated that energy tends to pass through a biological system as rapidly as possible except as constrained by dissipative structures.

Action in physics is computed from the difference between the kinetic energy (KE) and the potential energy (PE) at each point in the system's trajectory, integrated over the path between the points of reference:

$$\text{Action} = S = \int_{t_1}^{t_2} (\text{KE} - \text{PE})\, dt.$$

The path of the system can then be described as that for which the action has the least value (Feynman 1963; Watson 1986).

It is evident from the observation of ecological systems that living organisms apparently contravene such a principle in the same way that they apparently contravene the second law of thermodynamics. In fact, living organisms, as shown above, assume a state of "least dissipation" which may be equally interpreted as a state of "most action": "most action" is the accumulation of the greatest energy content for the longest period of time possible. This may be categorized as the "principle of most action". "Most action" not only implies "least dissipation" but includes the additional biological characteristic whereby total energy assimilated also tends to increase.

Biological energy may be divided into "potential energy", the energy stored in the biomass, and "kinetic energy", the energy required to maintain that biomass. In biology, potential energy is comparable with the energy stored in a flywheel, rather than the energy of position. The kinetic energy is the energy input required to maintain the flywheel at constant angular velocity. Resonance tends to increase the energy stored, as a button on a loop of string can be caused to rotate ever faster by periodic pulls on each end of the loop.

It is postulated that ecosystems are structured on the opposition of two "action principles": the "principle of most action" induces the conservation of energy for the longest time possible whereas the "principle of least action" tends to accelerate energy dissipation and reduce biomass. "Least action" and "most action" thus function as opposing attractors.

Homeokinesis

A primary factor in the attainment of a state "most action" is the elimination of fluctuation. Elimination of fluctuation in a population is contingent on the maintenance of rela-

tively constant mean size and constant abundance. Stable populations are the evidence that this occurs. The physical basis for maintenance of uniformity is provided by the doctrine of homeokinesis: a physical science for complex systems (Soodak and Iberall 1978). Through symmetrical interaction the available free energy is uniformly distributed among interacting atomisms (indivisible thermodynamic engines). The interactional energy is not equipartitioned each collisional cycle, but instead the atomisms "internally time-delay, process and transform collisional inputs, generally using many fluid-like dissipative mobile steps" (Soodak and Iberall 1978). In living systems, where the thermodynamic engines have a finite life span, continuity of the interactive process demands cohesion within the population, expressed as group control of individual growth rate and population density, and desynchronization of the life cycle.

Ergodynamic Equilibrium

To have continued existence, forces within organisms and ecosystems must override the principle of least action and move toward a state of most action. It is "pull-devil-pull-baker" all the way as the opposing forces vie for dominance, with Le Chatelier's principle ensuring that the two attractors eventually reach equality and a relatively steady state. This process is recognized as "succession" (Drury and Nisbet 1973; McIntosh 1980, 1985). During early successional stages, species diversity increases and then decreases in the final stages as the steady-state climax is approached. In any state other than the climax, a viable ecosystem will move toward a state of increasing action. Dominance of the "most action" attractor is clearly manifest during the penultimate stages of succession as the dominant species increases its influence and subordinate species are eliminated. At the level of primary production, a trend to "most action" is indicated by Wiegert (1988). In the course of discussing alternative and distinct pathways of photosynthesis, he suggested that a specific pathway was selected because, in a given environment, overall net fixation of energy per unit area over time was increased and mortality decreased. Jean (1988), too, has shown that phyllotaxis in plants (the orderly arrangement of leaves on the stem of a plant) can be interpreted through the principle of "minimum entropy production".

At the climax, an ecosystem occupies an equilibrium position between the two opposing attractors, yet, at the same time, it is "far from [thermodynamic] equilibrium". Tansley (1935) referred to this as a state of dynamic equilibrium, but this is too close to "thermodynamic equilibrium" for this particular usage. The terms "steady state" and "stationary state" are too static in their implications; therefore the climax state seems best described one of "ergodynamic equilibrium" (Gnaiger 1983, 1986): equilibrium maintained through the performance of internal work.

The common characteristic of all ecosystems is that they are *climax seeking*.

Homeorhesis

The capacity of a biological system to stabilize itself may be described as "homeorhesis" (the stabilization of flows) (Waddington 1968) rather than "homeostasis" which implies the stabilization of a specific state. Homeorhesis expresses the climax-seeking characteristic of an ecosystem; it is the imperative to move toward a balance between the forces reducing energy dissipation under the "most action" attractor. The climax thus implies no specific state; it is merely the stabilization of input and output energy flows. This cannot be referred to as energy flux because input and output are quite different in nature (Kirkaldy 1965). This explains why, as Curtis and McIntosh (1951) stated,

> There are...no groups of tree species which regularly occur together, except for accidental duplications of very narrow environmental ranges.

Evolution and Natural Selection

Major features of evolution are an increase in the number of species and an increase in average complexity (Simpson 1953; 1969; Sepkoski et al. 1981). It is postulated that this increase in diversity (increased heterogeneity) has been stimulated by the principle of least action tending to increase energy flow through the system. Increased energy flow results from an increase in asymmetrical interaction between individuals of different species. This is most readily seen in heterotrophy (the consumption of one organism by another) which is the limiting form of asymmetrical interaction. Heterotrophy necessitates the performance of much work (and the dissipation of an equivalent amount of energy) in the conversion of the "potential" energy of one organism into that of another (Brody 1945): hence the greater the heterogeneity, the greater the energy dissipation. According to Stanley (1973), heterotrophy, which evolved in the late pre-Cambrian era, was responsible for the great diversity of species suddenly appearing in the Cambrian. For some 3 billion yr prior to the evolution of heterotrophy, life moved very slowly, and then, quite suddenly (by geological standards), a great increase in the rate of energy degradation transformed the system from a static state to a dynamic one and opened the floodgates of evolution. Since the Cambrian, diversity and rate of dissipation have generally increased although not monotonically.

Notwithstanding, an overall increase in heterogeneity is not the only recognizable evolutionary trend; for example, the increase in size, observable along numerous evolutionary lines, expresses the opposite effect. The biological world may thus be represented as a continuing struggle between homogeneity and heterogeneity, between the opposing trends to least and most action, in which the trend to homogeneity dominates system behaviour over successional or ecological time, whereas heterogeneity increases inexorably over the longer spans of evolutionary time, although punctuated at infrequent intervals by cataclysmic species reductions. After each cataclysm, flows stabilize through the successional process, if necessary, through the elimination of additional species. If life is to continue, the trend to most action must prevail over ecological time.

To accommodate these various facets of the biological process, it is necessary to postulate that over ecological time and within a specific complement of species forming an ecosystem, the dominating trend is toward most action and homogeneity. Any viable change resulting from genetic instability will induce either an increase or a decrease in the action, but given the long-term trend to least action, it is evident that the probability of any specific change leading to "least action" is somewhat greater than the probability that it will lead to "most action". In such a system, both total energy assimilated and the rate of energy dissipation increase

over the long term, resulting in more work done and more complex dissipative structures.

Dominant species exhibit maximum long-term energy conservation through high biomass and long life span (*K*-selected species) (MacArthur and Wilson 1967; Southwood 1977) whereas species at the other end of the spectrum emphasize maximum energy assimilation (frequently in a specialized environment) and short generation time (*r*-selected species). Both ends of the spectrum follow the path of increasing action, but "*K*-selected" species emphasize the time component whereas "*r*-selected" species emphasize energy acquisition. Pacific salmon epitomize extreme energy acquisition and a highly synchronized life history.

When confined together the various species form a hierarchy in which their relative ability to acquire and conserve energy determines their continued existence and position in the system hierarchy. In such circumstances, time is the determining factor. This is in accordance with theory which states that a hierarchy can be ordered only on the basis of reaction time: the higher in the hierarchy, the longer the reaction time (Bastin 1968; Simon 1973; O'Neill et al. 1986).

Natural selection results from the interaction of these two opposing processes, combined with the competitive effect induced by the differential damping of environmental signals. The more heavily damped a resonator, the wider is the band of signals to which it can respond and the more will it tend to encroach on those less well damped. The dominant species, being the most heavily damped resonator, responds to the widest band of environmental signals, which is equivalent, as McNaughton and Wolf (1970) concluded, to the one with the broadest niche.

Thus, evolution results, not from a single attractor, but from the effect of two opposing attractors alternatingly storing and facilitating the dissipation of energy, as a good manager accumulates assets and then cuts away the "fat" and streamlines a company's operation, diverting the money saved to retooling with more effective equipment to meet the competition.

The Lake Reference System

The lake reference system can now be outlined in more detail: it is one which is completely autonomous and in which there is a relatively straight food chain from primary producer to terminal predator. Species assemble in response to the ambient set of environmental signals which are identified and damped. Primary producers become, in turn, signals for heterotrophs to identify as heterotrophs themselves become signals. In this manner, structure and heterotrophy are self-augmenting. The various species populations sort themselves into a hierarchy according to their individual capacities to increase the action. An incoming signal is increasingly damped as it passes along the food chain, thus leading to dominance of the terminal species.

In the forest reference system the primary producer is also the dominant species and the one most heavily damped; therefore, it exerts maximum control over the incoming signals.

Testing the Hypothesis

A hypothesis needs be tested to determine the limits of its applicability, but as Slobodkin (1964) stated:

> The normal criteria of scientific quality which we use as biologists are not the same as those of the physicist and mathematician....Empirical sciences must develop their own standard of quality and cannot take refuge from necessity of thought in the shadow of Newton or Euclid.

To this end, Peter Vanriel and I devised a test protocol, again centred on a small arctic lake, based on the following considerations.

Ulanowicz (1972) theorized that an increase in energy density along the food chain (measured in joules per gram) is a necessary condition for stability in an ecosystem. This is the exact opposite to what might be expected under the Second Law, yet must be faced if biological systems are to have a thermodynamic base. The proposition was extended by May (1973) to an indefinite number of trophic levels, and the theorem was subsequently reformulated by Hirata and Fukao (1977) to correct the direction of mass flow in Ulanowicz and May's theorem. They also added additional results on specific nutrient increase along the food chain. Further, Hirata and Ulanowicz (1984) pointed out that "in complex food webs, inversions in the hierarchy of energy density may occur in some parts of the food-web, but they will disappear during subsequent succession."

Dickie et al. (1988) showed that there is a general increase in size at each successive trophic level in the food chain of a simple ecosystem such as that of an arctic lake. It is also recognized that there is a decrease in the *P/B* ratio along the food chain (Winberg 1972; Winberg et al. 1972; Brylinsky and Mann 1973; Mann and Brylinsky 1975; Brylinsky 1980; Saunders et al. 1980). As the *P/B* ratio has been shown by MacArthur (Leigh 1965) to have the dimensions of time (= 1/mean life span), a decline in the *P/B* ratio indicates an increase in mean life span.

Space and time (size and age) should thus be included in an expanded view of energy density relationships in an ecosystem. An ecosystem may therefore be conceived as a hierarchy in which the action, which is equivalent to energy density in the expanded sense, increases along the food chain.

Four routes, therefore, are open to effect an increase in action: (i) an increase in simple energy density (sensu Ulanowicz), (ii) an increase in mean life span, (iii) an increase in individual size (biomass), and (iv) an increase in the number of individuals per unit area. All but the first condition have been shown to be true by observation; therefore, confirmation of theory would be provided by showing that the first also is true for a specific ecosystem.

To this end, we examined the energy density relationships between identifiable trophic levels in Keyhole Lake (Vanriel 1989).

In the event, the hypothesis was fully substantiated: energy density (in joules per gram) increased from primary producing algae to the terminal predator, Arctic char (Fig. 13). The only apparent anomaly occurred in the zooplankton, which consistently showed a higher energy density than all other species. In that zooplankton do not form a significant fraction of the diet of Arctic char (Fig. 14), it seems that planktonic interactions exist in what is essentially a separate compartment of the ecosystem, until death of the plankton brings them into the detrital stream.

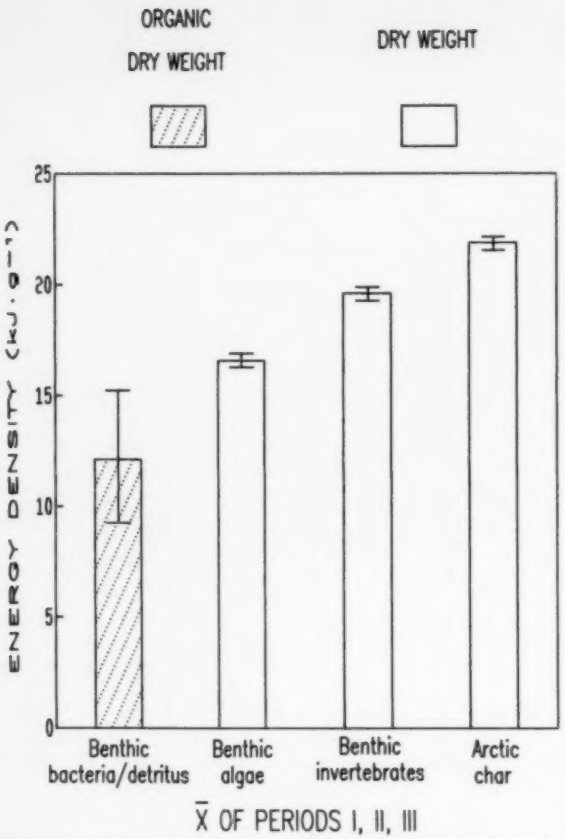


FIG. 13. Increase in energy density (joules per gram) along the trophic hierarchy, Keyhole Lake, Northwest Territories. Zooplankton are not included because they form a very small fraction of the diet of Arctic char. (From Vanriel 1989)

Discussion

This formulation of biosystem thermodynamics is different from others in several features. Perhaps the most important differences are (i) the introduction of action principles and thus the incorporation of time as a dimension, rather then a simple indication of direction ("time's arrow"), as in classical thermodynamics, and (ii) the concept of two opposing attractors dominating ecosystem behaviour in two different time frames. In the short term, systems tend to most action (maximum assimilation, least entropy production, and least work), but owing to system malleability, over evolutionary time, the overall trend is to greater entropy production and increasing work done to maintain the system further and further from thermodynamic equilibrium. Increased assimilation of energy and more rapid energy dissipation allowed increased complexity (with respect to both individuals and systems) and increased stored information through (i) increased identification of environmental signals and (ii) self-augmentation of signal diversity through structure and heterotrophy. Over evolutionary time the ecosystem explores and dissects the total spectrum of environmental signals against the opposing trend of individual species to broaden the signal band to which it responds.

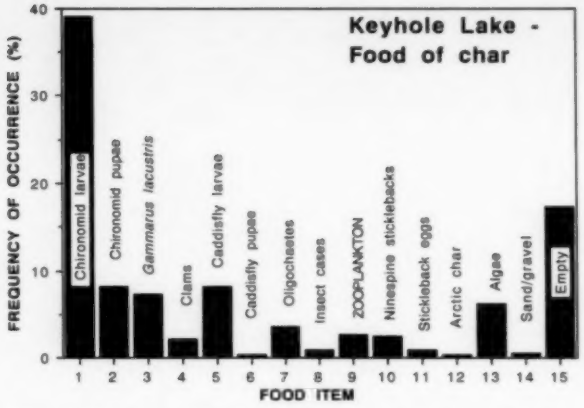


FIG. 14 Food of Arctic char, Keyhole Lake, Northwest Territories. (Redrawn from Vanriel 1989)

A further difference between the action hypothesis and a view commonly held is that a population functions as a cohesive unit, not merely as a collection of individuals. In general, it may be stated that symmetrical interaction among similar individuals leads to most action (or least dissipation). Least entropy production is contingent on uniform energy distribution (comparable with a state of maximum entropy). Asymmetrical interaction between individuals of different species tends to decrease action (increase entropy production). Symmetrical (neutral or mutually beneficial) interaction between different species allows coevolution. As Pasteur said, life began as an asymmetry, but an asymmetry within a greater symmetry.

The climax, or ergodynamic equilibrium, thus represents a state of both minimum and maximum work, depending on the viewpoint. It is the maximum attained at a given point in time from an evolutionary point of view, for a particular environment and species complex, but it is also the minimum attainable given the present components in the immediate environment. The climax may thus be described as a "minimax" (Lotka 1924, 1945; Kirkaldy 1965).

When one moves beyond the confines of the autonomous system into an open system with seasonally and periodically variable environments, the situation becomes unbearably complex.

An alternative hypothesis favoured by Jørgensen and Mejer (1979, 1981), Kay (1984, 1991), Kay and Schneider (1992), and Nielsen (1992) postulates that systems tend toward maximum "exergy", where "exergy" is a measure of the maximum work that can be extracted from a system if it is allowed to come to equilibrium with its surroundings: exergy, in effect, measures the quality of the energy (Kay 1984).

Conclusion

The current view among forest ecologists appears to be that small-scale cycles of regeneration and change give rise to a hierarchy of cycles of different length, occurring continually in different regions of time and space, each contributing to the dynamic ensemble (O'Neill et al. 1986). At the top level, the characteristics of the dominant species largely reflect the stability characteristics of the ecosystem as a whole

(Frank 1968) and at the same time impart "top-down" stability. Species at the lowest level in the hierarchy have a life cycle that is but an instant in time compared with the life cycle of the forest dominant. This short life cycle allows a rapid response to changes in energy availability. A large number of species in a fluctuating environment can thus acquire the greatest amount of energy possible, with great efficiency. A rapid, flexible response is thus an important factor in survival at the lower hierarchical levels, a characteristic largely denied the heavily time-damped dominants.

At the world level, the whole biosystem functions as a closed system constrained by the energy assimilated and the biosphere boundaries. Over long periods of evolutionary time, boundaries at all levels impose a degree of stability on the biosystem ensuring that a state close to ergodynamic equilibrium is reached. When cycles at any level are disrupted the whole system is affected, but the higher up the hierarchy at which cycles are disturbed, the greater will be the resultant effect on the system. Once initial relationships in a relatively autonomous system are destroyed by removal of preexisting boundaries, the system will tend to fluctuate in the absence of external constraints; hence, its behaviour will be largely unpredictable. Intermittent but severe disruption of existing ecosystems has occurred over evolutionary time, but once the disrupting factor declined or was eliminated, the homeorhetic mechanism stabilized flows at a new level, irrespective of the magnitude or nature of the catastrophe.

Difficult though it may be to translate this hypothesis into a useful management strategy, if these are the facts of the case, and they form an internally consistent whole, then we must accept them if we wish to manage ecosystems effectively. We have to think in terms of systems governed by laws that are different from Newtonian precepts or narrow extrapolations of the Second Law. As products of Western philosophy, and especially as scientists, we have been indoctrinated from our youth to think in Newtonian terms. In fact, thinking in such terms used to be one of the essential qualifications of a scientist. However, this is changing rapidly at the cutting edge of physics; observed events at new levels of investigation have frequently been found to confound previously established principles and notions.

I like to think that biological and physical theory may eventually be united at some deep level, for the quantum of "action" is Planck's constant (6.62×10^{-34} J-s); it all began when the first photon was time-delayed. But, unlike that of particle physicists, our perception of reality will greatly affect the future of our world and we (and future generations) will have to bear responsibility for the translation of that perception into action of a more familiar kind.

There is obviously a large gap between deep theory and events observed in a specific population in a system of low autonomy. However, I believe that it is necessary to recognize the patterns at the general level before we can attempt to explain more specific events. If all events occur within the boundary conditions determined by thermodynamic relationships, we must gradually work inward from the circumference toward the centre, and also in the opposite direction, from the specific to the general, hopefully to meet somewhere in between. In the meantime, many crises will be upon us when our actions will have to be determined by the best knowledge possible of the system specifics, but guided by a clear formulation of general ecological principles. It seems certain that we shall never have enough information to manage ecosystems "scientifically"; therefore, I believe that it is necessary to develop an environmental ethic, based on the need to maintain near-symmetrical interaction between all species in the system. Asymmetry beyond certain limits will inevitably change an ecosystem from its original form, and beyond certain limits will be self-eliminating. As the motto of Finley Ecological Research, Sidney, states: "Cave justitiam naturae" — beware the justice of nature — it may be delayed but it is always certain and always evenhanded.

Immense problems face us if we are to convert the world from the present predominantly exploitative phase to a managed, sustainable regime, which seems to be the only viable alternative to further ecosystem degradation. To meet these difficulties, we need a new appreciation of the extreme complexity and delicacy of the systems we are presently, and all too frequently, thoughtlessly disturbing. Our only hope of escaping from the ecological problems with which we are beset is through improved knowledge, enormous effort, and independent thinking. As funding for basic research declines and biological problems increase in intensity, there will be an increased demand for public accountability, political direction of science, and simplistic solutions. By the very nature of our system, politicians will decide on the major problems to be investigated through control of funding, but scientists must have input into these decisions and be free to voice criticism without fear of retribution. Scientists must be free also to decide on how the selected problems should be investigated. It is therefore their duty to educate politicians and the public as to the nature and complexity of the real problems. Further, I believe that it is essential that more able scientists, after many years of toiling in field or laboratory, get involved in the administration of science. To ensure that these positions are attractive to top scientists, rather than anathema to them, incumbents must have the power to implement their ideas and concepts. A research administrator must have a vision of what he or she wishes to accomplish and the power to build an organization that will fulfil his or her scientific ambition. As dominant species, we have assumed too broad a niche and imposed too great an asymmetry on the rest of the biosystem for it to survive in its current configuration. Time, as in "action", is running very short.

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[3]The anadromous Arctic charr of Nauyuk Lake, N.W.T., Canada, p. 201–227. *In* H. Kawanabe, F. Yamazaki, and D.L.G. Noakes [ed.] Biology of charrs and masu salmon. Physiology and Ecology, Japan, Special Volume 1, Proceedings of the International Symposium on Charrs and Masu Salmon held at Sapporo, Japan, 3–9 Oct. 1988.

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Guide for Authors

Introduction

We welcome manuscripts reporting significant new information in fisheries and aquatic sciences. Manuscripts may concern cells, organisms, populations, ecosystems, or processes that affect aquatic production systems, and cover numerous disciplines including biology and ecology of marine and freshwater organisms, physiology, toxicology, genetics, limnology, oceanography, economics, disease, and management.

Manuscripts are selected for publication according to the extent and significance of new knowledge or ideas presented. Preference will be given to those whose experimental results emphasize causal mechanisms underlying observed phenomena rather than pure description and fact. Manuscripts should lead to identifiable conclusions or syntheses, which variously may amplify, modify, question, or redirect accumulated knowledge embodied in contemporary perceptions of a particular state of aquatic sciences. Their novelty must relate to more than the particular (a certain year, place, taxon, chemical compound) and their contribution to science must clearly be beyond the confirmatory state.

Manuscripts submitted should be as comprehensive as possible; research fragments are generally unacceptable. If a single paper cannot be produced, then closely related papers should be cross-referenced and submitted together.

The *Journal* considers the following types of contributions:

Articles: Studies of broad scope that are original contributions to science.

Reviews: Detailed critical appraisals of broad areas of investigation, particularly those that have developed rapidly in recent years.

Perspectives: Essays of opinion or hypothesis on aquatic science of concern to the professional and layperson. References are desirable; informal style is welcome.

Comments: Opinion on topics recently discussed in the *Journal*; preferred maximum length, 500 words.

Manuscript Submission

Submit manuscripts in triplicate to the Editor, *Canadian Journal of Fisheries and Aquatic Sciences*, Research Journals, National Research Council of Canada, Ottawa, ON K1A 0R6, Canada, accompanied by a covering letter that (1) states the main points and significance of the work, (2) avows that all coauthors fully participated in and accept responsibility for the work and that it is not being considered for publication elsewhere, (3) suggests potential referees, and (4) identifies other manuscripts containing the same or similar information. Original typescripts and figures (except halftones) are best retained by the author until requested. Packaging of manuscripts and illustrations should be robust enough to resist damage in transit.

Each manuscript is normally submitted to two referees for appraisal before final evaluation by an editor. However, the Editor will return unreviewed those manuscripts that do not fall within the *Journal's* editorial policy or scope.

Authors are requested to submit diskettes (with *accepted* manuscripts only) prepared on Macintosh or IBM-compatible personal computers. Include files in both your word-processing format and ASCII on a 3.5- or 5.25-in. disk. Please identify the word-processing software and version number used.

Editorial Practices

The *Council of Biology Editors Style Manual* (5td ed. CBE, 9650 Rockville Pike, Bethesda, MD 20814, USA) is used as the authority in matters of form. The standards for spelling are either *Webster's Third International Dictionary* or the *Oxford English Dictionary* and *Le Grand Larousse encyclopédique*. Authors are responsible for consistency in spelling. Titles of periodicals are abbreviated as in *Serial Sources for the BIOSIS Data Base* (BioSciences Information Service, Philadelphia, PA 19103, USA). Authors are responsible for ensuring the accuracy and completeness of their reference list. The *Journal* follows the names and spelling for fishes recommended in *A List of Common and Scientific Names of Fishes from the United States and Canada* (5th ed. 1991. Spec. Publ. No. 20, American Fisheries Society) and the gene nomenclature for protein-coding loci outlined in Shaklee et al. (1990. Trans. Am. Fish. Soc. 119: 2–15). All measurements must be metric, use SI symbols in most instances (exceptions noted in the editorial in the *Journal*, Vol. 40, No. 12), and adhere to the *Canadian Metric Practice Guide* CAN3-Z234.1-79 (Canadian Standards Association, 178 Rexdale Boulevard, Rexdale, ON M9W 1R3, Canada).

Series titles should be avoided. An abstract is required for all manuscripts and should state concisely, in up to 175 words, what was done, found, and concluded.

Proofs are sent to the author, who is responsible for correcting errors in typesetting. *Alterations to the content must be avoided.*

Preparation of Manuscripts

General Guidelines

Movement of manuscripts through review channels and the editorial office is greatly expedited if manuscripts are prepared in *Journal* style and format. When in doubt about specific details, consult a current issue of the *Journal*. General guidelines follow.

Type the manuscript on white paper (8.5 × 11 in.) on only one side of the page. Leave all margins at least 1 in. wide.

Type only the title, authors' names and affiliations, and related footnotes on the first page. Number all pages beginning with the title page, including those for tables and captions for illustrations.

Double-space all parts of the manuscript, including tables, captions for tables and figures, footnotes, and the reference list. Underline only material that is to be printed in italics.

Do not use all capitals anywhere in the manuscript.
Use the name-and-year system for literature citations.

Checklist for Manuscripts

Attention to the following questions will expedite appraisal of manuscripts by referees and editors.

Are the findings, interpretations, and conclusions adequately documented and relevant to the purpose of the study?

Are all the tables and figures needed, and organized to facilitate comparison? Are there inconsistencies between tables and figures and the text, or within the text? Should some of the data be made available separately in a data or manuscript report or at a data repository?

If statistical analysis is included, is it subordinate to the research? When probability statements are made, are only the statistical tests cited and unnecessary statistical tables excluded?

Would any of the text be clearer if condensed? Are summary statements given at the beginning of sections and paragraphs, and are details in sections and paragraphs relevant to their topics? Does the organization of the manuscript follow logically from the statement of purpose in the introduction?

Does the *title* encompass the content of the report? Does the *abstract* give the essentials of the new knowledge? Is the *introduction* largely limited to the scope, purpose, and rationale of the study? Is review of the literature limited to defining the problem? Are details of *materials and methods* limited to what readers need to understand the design of the study and to judge the adequacy of the data? Are generalizations from the *results* supported by the data provided? Are findings distinguished from inferences? Is the *discussion* limited to interpretation and significance of the findings?

The most common technical problems in submitted manuscripts are listed below. Authors can hasten the processing of their papers if they pay attention to these points during manuscript preparation.

(1) Insert bibliographic strip before the abstract (Authors, date, title, Can. J. Fish. Aquat. Sci.).

(2) Limit abstract to one paragraph of about 175 words.

(3) Double-space all elements of the manuscript, including references, table captions, and figure legends.

(4) Avoid exclusive use of capitals anywhere in the manuscript, including headings, table captions, and figure legends.

(5) Underline only Latin names of organisms and certain statistical and mathematical notation to indicate italics.

(6) Use correct SI symbols for units or measure in figures, tables, and text. Place a zero before the decimal for numbers less than unity.

(7) Avoid ambiguous forms such as g $C/m^2/d$; use g $C \cdot m^{-2} \cdot d^{-1}$.

(8) Identify test used to test statistical significance and give probability value. No reference is needed for common statistical tests.

(9) In the text, generalize from tables and figures; avoid repeating all the details. Be sure each table and figure can stand on its own and is referred to in the text in numerical order. The captions should explain the purpose of the table or figure.

(10) Include acknowledgements section at manuscript stage, not when page proofs arrive.

(11) Provide the person's initials and mailing address when referring to personal communications.

(12) Delete unnecessary references that do not apply directly to the problem.

(13) Check references carefully against test citations and vice versa to ensure exact correspondence. Provide an availability statement for less easily retrieved material, e.g., available from Department of Economics, Simon Fraser University, Burnaby, BC V5A 1S6, Canada.

(14) Delete commas between name and date in citations such as (Smith 1990) and do not underline "et al."

(15) Replace 10^n in table headings and figure axes with appropriate SI prefixes or use words (e.g., thousands).

(16) Photocopies of figures, except halftones, are appropriate for review purposes. Send photographic prints or laser printouts of figures, or originals if they do not exceed 8.5 × 11 in., on request for publication. Use the same type of lettering throughout if possible.

Parts of the Manuscript

Organization

Organize the manuscript on the basis of the purpose or scope of the study as stated in the introduction. Ensure that the title and headings are in harmony with the statement of purpose.

Before writing any of the manuscript, list tentative headings in as few ranks as possible. Rework them until they appear to allow logical development for the reader; usually, chronological order is not effective. The findings will be more readily appreciated if methods, findings, and discussion are given in separate sections.

Organize tables and figures to facilitate comparisons, grouping related data in as few tables and figures as feasible. As far as possible, make the tables and figures clear without reference to the text.

Begin sections and paragraphs with topic sentences containing generalizations that lead readily to the particulars. Giving a conclusion first and then supporting it not only improves readability but also facilitates assessment by other scientists. Failure to give the most newsworthy generalizations first is one of the most prominent shortcomings in presentation of manuscripts.

See that everything in each section is relevant to the heading, and everything in each paragraph to the topic (opening) sentence.

Before writing any paragraphs, try writing the topic sentences for all of them and arranging these in appropriate order.

Title

Limit the title to what is documented in the manuscript. It is the key to the article and should clearly and concisely reveal what appears in the paper itself. The title serves two functions: (1) it allows the reader to judge whether or not the article is of potential interest and (2) it should provide enough information to permit the reader to judge the scope and potential importance of the article. Words in the title should convey a maximum amount of information and identify the nature of the research, organism used, and where appropriate, the technical approach (e.g., X ray, chromatography, mathematical analysis). Titles should not begin with a numeral or introductory prepositions such as "On" or "Towards" or expressions such as "A contribution to..."

or "Investigations on..." Good titles greatly assist scientists and librarians in using scientific literature and aid indexers in preparing titles for keyword indexes.

Abstract

The abstract should succintly mirror the contents and emphasis of the paper in about 175 words. Like the title, the abstract enables readers to determine the paper's content and decide whether or not they need to read the entire article. Begin the abstract with the main conclusion from the study, and support it with the relevant findings. Limit details of methods to those needed in understanding what was done, and work them into statements of findings. Avoid using phrases such as "...is discussed" or "...was found"; be specific. As the abstract is often divorced from the main body of the paper by abstracting and indexing services and is the only part of a paper some readers ever see, it is important that it accurately reflect the paper's contents and be completely self-contained (i.e., any *essential* references) in a retrievable form (e.g., R.B. Deriso. 1980. Can. J. Fish. Aquat. Sci. 37: 268–282).

Introduction

Limit the introduction largely to the scope, purpose, and rationale of the study. Restrict the literature review and other background information to that needed in defining the problem or setting the work in perspective. Try beginning with the purpose or scope of the work, defining the problem next, and adding guideposts to orient the reader. An introduction generally need not exceed 375–500 words.

Materials and Methods

Materials and Methods provides the framework for getting answers to the questions posed in the purpose of the work.

Limit the information on materials and methods to what is needed in judging whether the findings are valid. To facilitate assessment, give all the information in one section when possible. Refer to the literature concerning descriptions of equipment or techniques already published, detailing only adaptations. Often, it helps to begin statements on procedures with a phrase indicating the purpose, such as "To determine...we..." If the section is long, consider using subheadings corresponding to headings for the findings.

Results

Limit the results to answers to the questions posed in the purpose of the work, and condense them as comprehensively as possible. Give the findings as nearly as possible in the terms in which the observations or measurements were made and so avoid confusion between facts and inferences. State noteworthy findings to be noted in each table and figure, and avoid restating in the text what is clear from the captions. Material supplementary to the text can be archived in the report literature or a recognized data depository and referenced in the text.

Discussion

Limit the discussion to giving the main contributions of the study and interpreting particular findings, comparing them with those of other workers. Emphasis should be maintained on synthesis and interpretation and exposition of broadly applicable generalizations and principles. If these are exceptions or unsettled points, note them and show how the findings agree or contrast with previously published work. Limit speculation to what can be supported with reasonable evidence. End the discussion with a short summary of the significance of the work and conclusions drawn. If the discussion is brief and straightforward, it can be combined with the results section.

Acknowledgments

We strongly urge authors to limit acknowledgments to those who contributed substantially to scientific and technical aspects of the paper, gave financial support, or improved the quality of the presentation. Avoid acknowledging those whose contribution was clerical only.

References

References should be selected judiciously and be largely restricted to significant, published literature. References to unpublished data, manuscripts in preparation or submitted to other journals, progress reports, and unpublished papers given at annual meetings may not be cited in the reference list but may be noted in the text as unpublished data or personal communications (include mailing addresses). If consultants' reports or other documents of limited circulation must be cited, they should carry with them an availability statement explaining where the document can be obtained. Citations of literature in the text should be carefully checked against those in the reference list and vice versa to ensure exact correspondence. Nearly every manuscript submitted to the *Journal* contains errors in the references.

Tables

Tables are used to present repetitive data and should be as economical of space as possible.

Design tables to fit a 1-, 1½-, or 2-column width of the *Journal*.

Type each on a separate page and number with arabic numerals.

Use horizontal lines above and below the headings and below the columns, and seldom elsewhere. Never use vertical lines; leave extra space instead.

Table captions should be succinct and identify the purpose of the table sufficiently well to allow the table to stand on its own.

Indicate table footnotes by superscript lowercase letters and type them below the table.

Place the tables after the list of references.

Where each table is first referred to, type in the margin "Table — near here."

Note that *text tables* are not numbered, are typed within the text, and seldom need horizontal lines.

Figures

Provide photographic reproductions, laser printouts, or the original artwork (no larger than 8.5 × 11 in.) of each illustration. If submitting photographs, type the author's name and figure name on a strip of paper and fasten to the back of the print. Do not write on the illustration itself.

Provide two photocopies of line illustrations and two sets of any photographs for review purposes.

Design figures to fit a 1-, 1½-, or 2-column width of the *Journal* and ensure that all lettering, numerals, and symbols are legible, neat, and at least 1.5 mm high when reduced. Figures should not be mounted, stapled, or clipped. When possible, figures should be grouped and be done with the same or similar type of lettering.

Type legends in succession on a separate page. Add bar scales to maps, photomicrographs, equipment diagrams, etc.

Where each figure is first referred to, type "Fig. — near here."

Computer-generated figures produced on laser printers are acceptable; figures produced on dot matrix printers are not acceptable. If sheets of printed characters are used, be sure they adhere completely.

Draft rather than type axis labels for graphs.

Color plates are very expensive to produce and should only be used where the color being presented is essential to the understanding of the text. Extra costs for the reproduction of color plates are charged to the author. Submit only photographs of the highest quality for color reproduction. We prefer to use color photographs, but will accept drawings, color negatives, slides, or film positives.

Mathematical Expressions, Equations, and Formulae

Leave three spaces above and below lines that have much superscript material, and above and below equations and formulae. In the various expressions, place each component in its correct position.

Show all symbols clearly. In the margin, spell out Greek letters the first time they occur, and distinguish between lowercase *l* and the numeral *one*, and between capital *O* and the numeral *zero*. Make other explanatory notes similarly.

Appendix

Abbreviations

Abbreviate terms denoting units of weight and measurement in the text only when they are preceded by numerals.

becquerel	Bq
calorie	cal
centimetre	cm
centimetre, square	cm^2
centimetre, cubic	cm^3
centimetres per gram per second	$cm \cdot g^{-1} \cdot s^{-1}$
coulomb	C
day	d
decimetre	dm
degree Celcius	°C
degrees of freedom	df
gram	g
hectare	ha
hertz	Hz
hour	h
joule	J
kilometre	km
litre	L
lumen	lm
lux	lx
metre	m
metre, square	m^2
metre, cubic	m^3
micrometre	µm
milligram	mg
millilitre	mL
millimetre	mm
millimetre, square	mm^2
minute	min
molar mass	M
mole	mol
moles per litre	mol/L, M
month	mo
Pascal	Pa
second	s
standard deviation	SD
standard error	SE
tonne (metric ton)	t
volt	V
volume	vol
watt	W
week	wk
year	yr

Dates

Dates may be written in the sequence day-month-year without internal punctuation (On 9 October 1983 the...), or the alternative sequence month-day-year may be used with the year offset by commas (On October 9, 1983, the...).

Reference Citations in Text

Name-and-year system

The *Journal* uses the name-and-year system of citation; that is, the surname of the author(s) and the year of publication are inserted in the text at an appropriate point: "Brown (1983) compared..." or "...were compared (Brown 1983)." If the reference has more than two authors, include only the surname of the fist author followed by "et al." (not italicized)... "Brown et al. (1983) compared..." or "...were compared (Brown et al. 1983)."

Personal communications

Personal communications are not listed in the reference list. Using parentheses in the text, state the name and mailing address of the communicator followed by "personal communication."

Unpublished data

If an unpublished book or article has been accepted for publication, list it in the reference list section followed by the notation "(In press)." Only those manuscripts that are in galley or page proof stage or for which there is an acceptance letter can be considered in press. If an article is submitted but not yet accepted, state the name and address of the author of the unpublished material followed by the notation "unpublished data" in the text and do not include it in the reference list.

Reference Lists

The following bibliographic citations illustrate the punctuation, style, and abbreviations (according to *Serial Sources for the BIOSIS Data Base*) for references.

Journal article

PETERMAN, R.M. 1982. Model of salmon age structure and its use in preseason forecasting and studies of marine survival. Can. J. Fish. Aquat. Sci. 39: 1444–1452.

Entire issue of journal

GORDON, D.C. JR., AND A.S. HOURSTON [ED.] 1983. Proceedings of the Symposium on the Dynamics of Turbid Coastal Environments. Can. J. Fish. Aquat. Sci. 40(Suppl. 1): 365 p.

Book in a series

SCOTT, W.B., AND E.J. CROSSMAN. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184: 966 p.

Book not in a series

LEBLOND, P.H., AND L.A. MYSAK. 1978. Waves in the ocean. Elsevier, New York, N.Y. 602 p.

Part of book

HEALEY, M.C. 1980. The ecology of juvenile salmon in Georgia Strait, Britsh Columbia, p. 203–229. *In* W.J. Neil and D.C. Himsworth [ed.] Salmonid ecosystems of the North Pacific. Oregon State Unversity Press, Corvallis, Oreg.

Corporate author

AMERICAN PUBLIC HEALTH ASSOCIATION, AMERICAN WATER WORKS ASSOCIATION, AND WATER POLLUTION CONTROL FEDERATION. 1975. Standard methods for the examination of water and wastewater. 14th ed. Washington, D.C. 1193 p.

Theses

KUTTY, M.N. Some studies on the respiratory quotient in goldfish and rainbow trout. Ph.D. thesis, University of Toronto, Toronto, Ont. 102 p. Natl. Libr. Can., Can. Theses Microfilm No. 646.

Reports

SMITH, J.E. 1981. Catch and efforts statistics of the Canadian groundfish fishery on the Pacific coast in 1980. Can. Tech. Rep. Fish. Aquat. Sci. 1032: 90 p.

Translation

KOIKE, A., AND OGURA. 1977. Selectivity of meshes and entrances of shrimp traps and crab traps. J. Tokyo Univ. Fish. 64: 1–11. (Transl. from Japanese by Can. Transl. Fish. Aquat. Sci. 4950, 1983)

Time

A colon should be used as the separator between hour and minute and between minute and second. The symbols "h", "min," and "s" are not used, since they are symbols for hour, minute, and second in the sense of duration or the length of time. Thus, "12 h 30 min" expresses a measured time of twelve hours and thirty minutes duration whereas 12:30 refers to the time of day.

Word List

The spelling of the following words is frequently inconsistent in submitted manuscripts. We prefer that authors adhere to the *Journal's* house style for these commonly used terms:

age-class (n.)
aquaculture (n.)
Arctic char (n.)
brackish water (n.)
brackish-water (adj.)
chi-square (n., adj.)
cold water (n.)
cold-water (adj.)
deep sea (n.)
deep-sea (adj.)
deep water (n.)
deepwater (adj.)
freshwater (n., adj.)
fresh water (n.)
groundwater (n., adj.)
hard water (n.)
hardwater (adj.)
headwater (n., adj.)
lake water (n., adj.)
meltwater (n., adj.)
open water (n.)
open-water (adj.)
percent (n.)
salt water (n.)
saltwater (adj.)
sea-run (adj.)
seawater (n., adj.)
shallow water (n.)
shallow-water (adj.)
size-class (n.)
snowmelt (n.)
soft water (n.)
softwater (adj.)
tidewater (n., adj.)
t-test (n., adj.)
warm water (n.)
warmwater (adj.)
year-class (n.)
young-of-the-year (n., adj.)

Guide des auteurs

Introduction

Les manuscrits comportant une information nouvelle dans le domaine des sciences halieutiques et aquatiques sont les bienvenus. Ils peuvent se rapporter aux cellules, aux organismes, aux populations, aux écosystèmes ou aux processus qui influencent les systèmes de production aquatiques, et couvrir de nombreuses disciplines, y compris biologie et écologie des organismes marins et dulçaquicoles, physiologie, toxicologie, génétique, limnologie, océanographie, économique, maladies et gestion.

Les critères de sélection des manuscrits dépendent de l'étendue et de l'importance des connaissances ou idées nouvelles qu'ils contiennent. On donnera la préférence à ceux dont les résultats expérimentaux font ressortir les mécanismes sousjacents aux phénomènes observés plutôt qu'une simple description ou énoncé de fait. Ils doivent aboutir à des conclusions ou synthèses précises qui, de diverses façons, peuvent accroître, modifier, remettre en question ou réorienter le bagage actuel des connaissances et perceptions dans une discipline donnée des sciences aquatiques. L'originalité doit dépasser le caractère particulier (une année, un endroit, un taxon ou un composé chimique donné) et tenir à une épuration ou à une reformulation des connaissances actuelles en faisant plus que corroborer des faits.

Les manuscrits soumis devraient être aussi complets que possible; des fragments de recherche sont généralement inacceptables. S'il est impossible de produire un seul article, on devra soumettre ensemble des articles étroitement liés entre eux, avec références croisées. L'article ne doit pas avoir été soumis ou accepté pour publication ailleurs.

Le *Journal* considère les types de contributions suivants :

Articles : études d'une portée générale, constituant des contributions inédites à la science.

Critiques : appréciations critiques détaillées de vastes champs de recherche, particulièrement dans les domaines ayant connu de rapides progrès au cours des dernières années.

Perspectives : essais portant sur une opinion ou une hypothèse relative aux sciences aquatiques qui intéressent professionnels et profanes. Il est préférable de donner des références et d'écrire, si possible, dans un style simple.

Commentaires : opinions sur des sujets récemment exposés dans le *Journal*, et, de préférence, ne dépassant pas 500 mots.

Soumission des manuscrits

Les manuscrits doivent être soumis au rédacteur, *Journal canadien des sciences halieutiques et aquatiques*, Conseil national de recherches du Canada, Ottawa, ON K1A 0R6, Canada, en triplicata et accompagnés d'une lettre qui fait état 1) des principaux points et de l'importance du travail, 2) de la participation de tous les auteurs au manuscrit, de leur approbation de ce dernier et de l'assurance que le manuscrit en question n'est pas en cours d'examen aux fins de publications dans une autre revue, 3) de suggestions quant aux arbitres éventuels et 4) d'une mention d'autres manuscrits contenant une information identique ou qui se rapproche de celle contenue dans le manuscrit soumis. L'auteur devra, de préférence, conserver les originaux du texte dactylographié et des figures (sauf les similis) jusquà ce qu'on les lui demande. Afin de les protéger lors de l'expédition, les manuscrits et les illustrations doivent être solidement emballés.

Un manuscrit est normalement soumis à deux arbitres pour évaluation, avant l'évaluation finale par un rédacteur. Cependant, les manuscrits qui ne répondent pas à la politique éditoriale ou à la portée du *Journal* sont retournés à l'auteur sans avoir été soumis à l'arbitrage.

Les auteurs sont vivement encouragés à soumettre, en plus de la copie imprimée, une copie sur disquette (3,5 ou 5,25 pouces) du manuscrit (version *acceptée* uniquement) préparée en logiciel de traitement de texte (accompagné d'une filière en format ASCII) sur ordinateur Macintosh our sur ordinateur personnel compatible à l'IBM. Le logiciel de traitement de texte et le numéro de version doivent être identifiés.

Dispositions générales

Le *Council of Biology Editors Style Manual* (5^{e} éd., CBE, 9650 Rockville Pike, Bethesda, MD 20814, USA) sert de guide quant à la forme de la présentation. Le *Webster's Third International Dictionary* ou l'*Oxford English Dictionary*, et le *Grand Larousse encyclopédique* font autorité pour l'orthographe des mots. L'uniformité de cette dernière est la responsabilité des auteurs. Les titres de périodiques sont abrégés suivant les *Serial Sources for the BIOSIS Data Base* (BioSciences Information Service, Philadelphia, PA 19103, USA). C'est la responsabilité des auteurs de s'assurer que leurs références sont complètes et exactes. Pour les noms de poissons et leur orthographe, le *Journal* suit les recommandations contenues dans *A List of Common and Scientific Names of Fishes from the United States and Canada* (5^{e} éd. 1991. Spec. Publ. No. 20, American Fisheries Society). Pour la nomenclature génétique pour les locus de codage des protéines, le *Journal* suit les recommandations contenues dans Shaklee et al. (1990. Trans. Am. Fish. Soc. 119 : 2–15). Toutes les mesures doivent être conformes au système métrique et, dans la plupart des cas, être exprimées en unités SI (sauf exceptions mentionnées dans un éditorial du *Journal*, vol. 40, n^{o} 12), et se conformer au *Guide canadien de familiarisation au système métrique* CAN3-Z234.1-79 (l'Association canadienne de normalisation, 178, boul. Rexdale, Rexdale, ON M9W 1R3, Canada).

On devra éviter les titres en séries. Un résumé doit accompagner chaque texte et exposer brièvement, en 175 mots ou moins, ce qui a été fait, ce qui a été découvert et les conclusions auxquelles on est arrivé.

L'auteur doit revoir les épreuves qu'on lui remet et en corriger les erreurs typographiques. *Il doit éviter de modifier le contenu du texte.*

Préparation des manuscrits

Directives générales

La marche des manuscrits à travers les diverses étapes de l'arbitrage et de la révision sera grandement facilitée si les articles sont préparés dans le style et le format du *Journal*. En cas de doute sur des points particuliers, veuillez consulter une livraison récente du *Journal*. On trouvera ci-dessous des directives générales.

Dactylographiez le manuscrit sur papier blanc (mesurant 8,5 sur 11 pouces) sur un côté de la page. Laissez toujours une marge d'au moins 1 pouce.

Sur la première page, dactylographiez le titre, les noms et affiliations des auteurs et les renvois qui s'y rapportent. Numérotez toutes les pages, à commencer par la page-titre, de même que celles contenant les tableaux et les légendes des illustrations.

Tout le manuscrit, y compris tableaux, légendes des tableaux et des figures, renvois et liste de références, doit être dactylographié à double interligne. Ne soulignez que les mots qui devront être imprimés en italique.

En aucun endroit du manuscrit n'écrivez entièrement en majuscules.

Pour les références citées dans le texte, utilisez le système nom et année.

Liste de contrôle pour manusrits

Une attention particulière aux questions suivantes facilitera l'évaluation des manuscrits par les arbitres et les rédacteurs.

Les découvertes, interprétations et conclusions sont-elles bien documentées et pertinentes aux buts de l'étude ?

Les tableaux et figures sont-ils tous nécessaires et agencés pour faciliter les comparaisons ? Y a-t-il contradiction entre les tableaux ou les figures et le texte, ou à l'intérieur du texte ? Est-ce que certaines données devraient être présentées séparément dans un rapport manuscrit ou dans un dépôt de données ?

Si vous faites une analyse statistique, la statistique cède-t-elle le pas à la recherche ? Dans des énoncés de probabilité, seuls les tests statistiques sont-ils cités, et les tableaux statistiques inutiles sont-ils exclus ?

Le texte y gagnerait-il en clarté s'il était plus condensé, en tout ou en partie ? Contient-il des exposés sommaires au début de chaque section ou paragraphe, et les détails de ces sections et paragraphes sont-ils pertinents au sujet traité ? La marche du manuscrit est-elle conforme à la logique énoncée dans l'introduction ?

Le *titre* est-il représentatif du contenu du rapport ? Le *résumé* donne-t-il l'essentiel des connaissances nouvelles ? L'*introduction* se limite-t-elle à une esquisse de la portée, du but et des raisons de l'étude ? La revue de la littérature se limite-t-elle à la définition du problème? La section *matériel et méthodes* contient-elle le minimum de détails qui permettront aux lecteurs de saisir les grandes lignes de l'étude et de juger de la valeur des données ? Les généralisations sur les *résultats* sont-elles adéquates ? Permettent-elles de distinguer entre constatations et déductions ? La *discussion* est-elle limitée à l'interprétation et à l'évaluation des découvertes ?

Sont énumérés ci-dessous des façons d'éviter les problèmes techniques les plus communs dans la soumission des manuscrits. En accordant une attention particulière à ces points lors de la préparation de leurs manuscrits, les auteurs peuvent accélérer le traitement des articles.

1) Insérez la bande bibliographique avant le résumé (auteurs, date, titre, Can. J. Fish. Aquat. Sci.).

2) Limitez le résumé à un paragraphe d'environ 175 mots.

3) Dactylographiez à double interligne tous les éléments du manuscrit, y compris les références et les légendes des tableaux et des figures.

4) Évitez partout l'emploi exclusif de majuscules, y compris dans les en-têtes et les légendes des tableaux et des figures.

5) Ne soulignez que les noms latins d'organismes et certaines notations statistiques et mathématiques, qui devront être imprimés en italique.

6) Dans les figures, les tableaux et le texte, exprimez les unités de mesure par leurs symboles SI propres. Pour les nombres inférieurs à l'unité, placez un zéro avant la virgule décimale.

7) Évitez les formes ambiguës, telles que g C/m^2/d; utilisez plutôt g C·m^{-2}·d^{-1}.

8) Identifiez le test qui a servi à évaluer la signification statistique, donnant également la valeur de probabilité. S'il s'agit de tests communs, il n'est pas nécessaire den donner la référence.

9) Dans le texte, généralisez à partir des tableaux et des figures; évitez une répétition de tous les détails. Assurez-vous que tous les tableaux et figures sont indépendants et que, dans le texte, on y réfère dans l'ordre numérique. Les légendes doivent indiquer le but du tableau ou de la figure.

10) Préparez la section des remerciements au stade du manuscrit et non quand vous parviennent les épreuves.

11) En référant à des communications personnelles, donnez les initiales et l'adresse postale de la personne en cause.

12) Éliminez toutes références inutiles qui ne s'appliquent pas directement au problème.

13) Vérifiez soigneusement les références en regard des citations dans le texte et vice versa, afin de vous assurer qu'il y a correspondance. Dans le cas de matériel difficilement accessible, indiquez l'endroit où le trouver, p. ex. disponible auprès du Département d'économique, Université Simon Fraser, Burnaby, BC V5A 1S6, Canada.

14) Éliminez les virgules entre le nom et la date dans les citations telles que (Smith 1990) et ne soulignez pas *et al.*

15) Dans les en-têtes de tableaux et les axes des figures, remplacez 10^n par les préfixes SI appropriés ou utilisez des mots en clair (p. ex. milliers).

16) Aux fins de la révision, les photocopies des figures, sauf les similis, sont appropriées. Sur demande, lorsqu'il s'agira de publier l'article, envoyez des photographies ou des imprimés laser des figures, ou encore les originaux, s'ils ne dépassent pas 8,5 sur 11 pouces. Utilisez autant que possible un lettrage uniforme.

Parties du manuscrit

Organisation

Organisez le manuscrit par rapport au but ou à la portée de l'étude, tels qu'énoncés dans l'introduction. Il est particulièrement important que le titre et les sous-titres soient en harmonie avec les objectifs.

Avant de commencer la rédaction du manuscrit, dressez une liste provisoire des sous-titres ou en-têtes, avec le moins de divisions possible. Retouchez-les jusqu'à ce qu'ils sem-

blent assurer, pour le lecteur, une marche logique; ordinairement, l'ordre chronologique ne sera pas satisfaisant. Il sera plus facile d'évaluer les résultats si vous décrivez méthodes, résultats et discussion dans des sections séparées.

Organisez les tableaux et les figures de façon à faciliter les comparaisons, groupant les données apparentées en aussi peu de tableaux et de figures que possible. Assurez-vous que ces derniers sont aussi clairs que possible sans référence au texte.

Commencez les sections et les paragraphes par des énoncés généraux qui aboutissent naturellement à des énoncés particuliers. Si vous donnez d'abord une conclusion que vous appuyez ensuite, non seulement votre travail sera plus facile à lire, mais aussi les autres scientifiques pourront plus aisément en évaluer les résultats. Dans la rédaction des manuscrits, le défaut le plus commun est d'omettre de donner, au début, les généralités les plus dignes de mention.

Voyez à ce que le matériel de chaque section soit pertinent à l'en-tête et que le matériel de chaque paragraphe se rapporte à la première phrase introduisant le sujet.

Avant de rédiger les paragraphes, composez la phrase-thème de chaque paragraphe et disposez ces phrases dans l'ordre approprié.

Titre

Limitez le titre à ce que le travail veut démontrer. C'est la clé de l'article, et il devrait montrer clairement et de façon concise ce qui est contenu dans le travail lui-même. Le titre a deux fonctions : 1) il permet au lecteur de juger si, oui ou non, l'article peut avoir un intérêt et 2) il devrait fournir suffisamment d'information pour permettre au lecteur de juger de la portée et de l'importance possible de l'article. Les mots du titre devraient fournir un maximum d'information et identifier la nature de la recherche, de l'organisme utilisé et, au besoin, la méthode d'approche technique (p. ex. rayons X, chromatographie, analyse mathématique). Les titres ne devraient pas commencer par un chiffre ou par des prépositions d'introduction telles que « Sur » ou « Vers », ou des expressions telles que « Contribution à...» ou « Recherche sur... ». De bons titres facilitent le classement des publications et leur utilisation par les scientifiques et les bibliothécaires.

Résumé

Le résumé doit refléter succintement le contenu et les points principaux de l'article en 175 mots environ. Comme le titre, le résumé permet aux lecteurs de prendre connaissance du contenu de l'article et de décider si, oui ou non, il leur faut lire ce dernier en entier. Indiquez au début du résumé la principale conclusion de l'étude et appuyez-la par des découvertes pertinentes. Ne donnez que les détails des méthodes nécessaires à la compréhension de ce qui a été fait et insérez-les dans l'énoncé des découvertes. Évitez l'emploi de phrases telles que « ...on y analyse » ou « ... a été trouvé »; soyez spéficique. Comme le résumé est souvent séparé du corps principal de l'article par les services d'analyse et de classement, et que c'est la seule partie d'un travail que certains lecteurs auront l'occasion de voir, il est important que le résumé reflète précisément le contenu du travail et qu'il soit complet en lui-même (c.-à-d. seule les références *essentielles* sont indiquées, sous forme retraçable, p. ex. R.B. Deriso. 1980. J. can. sci. halieut. aquat. 37 : 268–282).

Introduction

Limitez l'introduction à la portée, au but et à la raison de l'étude. Ne mentionnez que les travaux publiés et autres informations nécessaires à la définition du problème et à la perspective du travail. Commencez avec le but ou la portée du travail, définissez ensuite le problème et ajoutez ici et là des jalons qui aideront à orienter le lecteur. En général, une introduction n'a pas besoin de dépasser 375–500 mots.

Matériel et méthodes

Cette section renferme ce dont on a besoin pour trouver réponse aux questions soulevées dans les objectifs du travail.

Limitez les renseignements à ce qui est nécessaire pour juger de la validité des découvertes. Cette évaluation sera facilitée si vous présentez, autant que possible, toute l'information dans une section. S'il s'agit d'outillage ou de techniques déjà publiés, référez à ces publications et ne décrivez en détail que les adaptations. Il y a souvent avantage à commencer un énoncé des méthodes par une phrase qui en indique le but, comme : « Afin de déterminer...nous... ». Si la section est longue, songez à utiliser des sous-titres correspondant à ceux que vous utilisez dans la section des résultats.

Résultats

Limitez les résultats aux réponses apportées aux questions en rapport avec le but de l'étude; que ces réponses soient aussi complètes que possible, tout en étant concises. Exprimez ce que vous avez trouvé, autant que possible dans les mêmes termes que ceux dans lesquels les observations ou les mesures ont été faites, évitant ainsi de confondre faits et spéculations. En dégageant les généralités des tableaux et des figures, référez-y et évitez de répéter dans le texte ce que les légendres devraient exprimer clairement. Le matériel complémentaire au texte peut être classé dans les séries des rapports ou dans un dépôt de données reconnu, et on y référera dans le texte.

Discussion

Limitez la discussion à l'énoncé de la principale contribution de l'étude et à l'interprétation de découvertes particulières, les comparant avec celles d'autres auteurs. On continuera à mettre l'accent sur la synthèse et l'interprétation, ainsi que sur l'exposition de généralisations et de principes largement applicables. S'il s'agit d'exceptions ou de points douteux, notez-les et faites ressortir la manière dont vos résultats corroborent ou contredisent les travaux déjà publiés. Limitez la spéculation à ce que vous pouvez appuyer sur des preuves raisonnables. Terminez cette section par un court résumé de l'importance du travail et des conclusions auxquelles il a conduit. Si la discussion est brève et précise, elle peut être combinée avec les résultats en une seule et même section.

Remerciements

Nous recommandons fortement aux auteurs de limiter les remerciements aux personnes qui ont contribué d'une manière substantielle aux aspects scientifiques et techniques de l'article, fourni une aide financière ou amélioré la qualité de la présentation. Évitez de mentionner les personnes qui n'ont fourni qu'un travail de soutien.

Références

On choisira les références avec soin, les limitant aux publications importantes. On ne peut citer dans cette section les références à des données inédites, manuscrits en préparation ou soumis à d'autres périodiques, états des travaux et communications inédites présentées à des réunions annuelles. On peut toutefois les mentionner dans le texte à titre de données inédites ou de communications personnelles (incluant les adresses). Si l'on doit citer des rapports d'experts-conseils ou d'autres documents dont la distribution est limitée, on devra préciser l'endroit où l'on peut se les procurer. On doit s'assurer que les références mentionnées dans le texte correspondent à celles qui sont contenues dans la liste de références et vice versa. Presque tous les manuscrits soumis au *Journal* contiennent des erreurs dans cette section.

Tableaux

Les tableaux sont utilisés pour présenter des données qui se répètent et devraient occuper le moins d'espace possible.

Agencez les tableaux de façon qu'ils s'adaptent soit à 1, 1½ ou 2 colonnes du *Journal*.

Dactylographiez chaque tableau sur une page séparée et numérotez-les en chiffres arabes.

Tracez des lignes horizontales de part et d'autre des en-têtes et au-dessous des colonnes, mais rarement ailleurs. N'utilisez jamais de lignes verticales. Laissez plutôt des espaces supplémentaires.

Chaque tableau doit avoir une légende instructive, complète et indépendante.

Les renvois des tableaux doivent être indiqués par des minuscules suscrites dactylographiées au bas du tableau.

Placez les tableaux après la liste des références.

Quand on réfère à un tableau pour la première fois, on indique dans la marge du manuscrit « Tableau — près d'ici ».

Notez que les *tableaux dans le texte* ne sont pas numérotés et sont dactylographiés dans le corps du texte. Ils ont rarement besoin de lignes horizontales.

Figures

Fournissez des photographies, des imprimés laser ou les dessins originaux (pourvu qu'ils ne dépassent pas 8,5 sur 11 pouces) de chaque illustration. Dactylographiez le nom de l'auteur et le numéro de la figure sur une lisière de papier que vous collerez au dos. N'écrivez pas sur l'illustration même. Transmettez deux photocopies des dessins au trait et deux séries de photos qui serviront au moment de la révision.

Les dessins devront occuper une largeur de 1, 1½- ou 2 colonnes du *Journal*. Assurez-vous que tous les chiffres, lettres et symboles sont lisibles, clairs et mesurent au moins 1,5 mm de hauteur une fois réduits. Les figures ne devraient pas être montées, brochées ou fixées à l'aide de trombones. Autant que possible, elles devraient être groupées et préparées avec le même type de lettrage.

Dactylographiez les légendes, dans l'ordre, sur des feuilles séparées. Dans le cas de cartes, photomicrographies, diagrammes d'instruments, etc., ajoutez une échelle.

À l'endroit où chaque figure est mentionnée pour la première fois, inscrivez en marge « Fig. — près d'ici ».

Les illustrations produites par imprimantes laser sont acceptables; les illustrations produites par imprimantes par points ne sont pas acceptables. Si vous utilisez du lettrage instantané, veillez à ce qu'il adhère parfaitement.

Il vaut mieux dessiner que dactylographier les inscriptions relatives aux axes.

La production de planches en couleurs est très dispendieuse et on ne devrait utiliser celles-ci que lorsque les couleurs sont essentielles à la compréhension du texte. Les coûts supplémentaires de reproduction de planches en couleurs sont débités à l'auteur. Pour les reproductions en couleurs, ne soumettez que des photos d'excellente qualité. Nous préférons utiliser des photographies en couleurs, mais acceptons dessins, négatifs, diapositives ou positifs de films en couleurs.

Expressions, équations et formules mathématiques

Laissez trois espaces au-dessus et au-dessous des lignes portant des chiffres ou des lettres suscrits ou souscrits, ou encore au-dessus et au-dessous des équations et des formules. Placez chaque composante des différentes expressions dans la position qui lui est propre.

Indiquez clairement tous les symboles. Épelez en marge les lettres grecques, la première fois qu'elles apparaissent. Faites une distinction entre la lettre *l* et le chiffre *un*, et entre la majuscule *O* et le chiffre *zéro*. Insérez de la même façon toute autre note explicative.

Appendice

Abréviations

N'abrégez les termes désignant les unités de poids et mesures dans le texte que lorsqu'ils sont précédés d'un nombre.

an	an
année	a
becquerel	Bq
calorie	cal
centimètre	cm
centimètre carré	cm^2
centimètre cube	cm^3
centimetrès par gramme par seconde	$cm \cdot g^{-1} \cdot s^{-1}$
coulomb	C
décimètre	dm
degré Celcius	°C
degrés de liberté	dl
écart type	ET
électronvolt	eV
erreur type	ErT
farad	F
gramme	g
hectare	ha
hertz	Hz
heure	h
joule	J
jour	d
kilomètre	km
litre	L
lumen	lm
lux	lx
mètre	m
mètre carré	m^2
mètre cube	m^3
micromètre	µm

milligramme	mg
millilitre	mL
millimètre	mm
millimètre carré	mm^2
minute	min
mois	mo
masse molaire	M
mole	mol
moles par litre	mol/L, M
pascal	Pa
seconde	s
semaine	sem
tonne (métrique)	t
volt	V
volume	vol
watt	W

Dates

On écrira les dates dans l'ordre jour-mois-année, p. ex. 9 octobre 1983, sans virgule entre le mois et l'année.

Citations de références dans le texte

Système de nom et année

Le *Journal* utilise le système de nom et année, c.-à-d. que le nom de l'auteur ou des auteurs et l'année de publication sont insérés dans le texte à un endroit approprié : « Brown (1983) compare... » ou « ...on a comparé (Brown 1983) ». Si la référence comporte plus de deux auteurs, inscrivez le nom du premier auteur seulement, suivi de « *et al.* » : « Brown *et al.* (1983) comparent... » ou « ...on a comparé (Brown *et al.* 1983) ».

Communications personnelles

Les communications personnelles ne doivent pas être incluses dans la liste des références. Utilisez plutôt des parenthèses dans le texte, entre lesquelles vous indiquerez le nom et l'adresse de la personne en question, suivis de « communication personnelle ».

Données inédites

Si un livre ou un article inédit a été accepté pour publication, insérez-le dans la liste des références, avec la mention « (Sous presse) ». On ne peut considérer comme étant sous presse que les manuscrits au stade d'épreuves ou ceux couverts par lettre d'acceptation. Si un article a été soumis mais n'a pas encore été accepté, ne l'incluez pas dans la liste de références, mais indiquez le nom et l'adresse de l'auteur du matériel inédit, dans le texte lui-même, avec la mention « données inédites ».

Liste de références

La liste qui suit donne des exemples de ponctuation, de style et d'abréviations utilisés dans les références bibliographiques (d'après les *Serial Sources for the BIOSIS Data Base*).

Article du journal

ARCHAMBAULT, D. ET E. BOURGET. 1983. Importance du régime de dénudation sur la structure et la succession des communautés intertidales de substrat rocheux en milieux subarctiques. Can. J. Fish. Aquat. Sci. 40 : 1278–1292.

Numéro complet du journal

GORDON, D.C. JR., AND A.S. HOURSTON [ÉD.] 1983. Proceedings of the Symposium on the Dynamics of Turbid Coastal Environments. Can. J. Fish. Aquat. Sci. 40(Suppl. 1) : 365 p.

Livre dans une série

HILTON, J.W. ET S.J. SLINGER. 1981. Nutrition et alimentation de la truite arc-en-ciel. Publ. spéc. can. sci. halieut. aquat. 55 : 17 p.

Livre ne faisant pas partie d'une série

FORRESTER, W.D. 1983. Manuel canadien des marées. Ministère des Pêches et des Océans. Service hydrographique du Canada, Ottawa (Ont.). 148 p.

Partie d'un livre

AUBERT, M., J. AUBERT, S. DANIEL ET N. DESIROTTE. 1982. État actuel de la pollution bactérienne au large des côtes françaises, p. 36–40. *Dans* M. Ruivo [éd.] La pollution des mers et les ressources biologiques. Fishing News (Books) Ltd., Londres.

Corporation-auteur

AMERICAN PUBLIC HEALTH ASSOCIATION, AMERICAN WATER WORKS ASSOCIATION, AND WATER POLLUTION CONTROL FEDERATION. 1975. Standard methods for the examination of water and wastewater. 14th ed. Washington, D.C. 1193 p.

Thèse

DELISLE, C. 1969. Écologie, croissance et comportement de l'éperlan du Lac Heney, Comté de Gatineau ainsi que la répartition en eau douce du Québec. Thèse doctorale, Université d'Ottawa, Ottawa (Ont.). 161 p.

Rapports

DUTIL, D.J., M. FORTIN ET Y. VIGNEAULT. 1982. L'importance des zones littorales pour les ressources halieutiques. Mémoire remis au Conseil consultatif de l'environnement du Québec. Rapp. manuscr. can. halieut. aquat. 1653 : 29 p.

Traduction

KOIKE, A. ET OGURA. 1977. Selectivity of meshes and entrances of shrimp traps and crab traps. J. Tokyo Univ. Fish. 64 : 1–11. (Traduit du Japonais par Can. Transl. Fish. Aquat. Sci. 4950, 1983)

Temps

On devra séparer par deux points (:) heures et minutes, et minutes et secondes. Les symboles « h, » « min » et « s » ne seront pas utilisés car ils représentent heure, minute et seconde dans le sens de durée ou intervalle de temps de douze heures et trente minutes, alors que 12 : 30 se rapporte à l'heure du jour.

Liste de mots

Cette section, dans la version anglaise du Guide, contient une série de mots dont l'orthographe pose certains problèmes d'uniformité, comme, par exemple, « cold water » (n.), « cold-water » (adj.), « hard water » (n.), « hardwater » (adj.), etc. L'auteur préparant un texte en anglais est prié de consulter la version anglaise du Guide.

RESEARCH JOURNALS PUBLICATION POLICY

1. Mandate

The National Research Council Act confers on the National Research Council of Canada (NRC) the right to publish scientific and technical information.

The objective of NRC Research Journals is to publish high-quality scientific and engineering journals and monographs in a timely and cost-effective manner. The research journals and monographs published by NRC provide scientists and engineers in Canada and elsewhere with a means to communicate with their peers in the international research community. Both the Editors and Research Journals are committed to producing high-quality international publications, thereby adding a Canadian contribution to the world's research literature.

2. Rationale

Since NRC began the publication of research journals in 1929, numerous editorial practices and procedures have been developed on the basis of time-honoured traditions of the various disciplines. It is important that NRC follow the best current practices, and where possible, improve on them. This document reviews and formalizes the editorial and production policies and defines a set of ethical publication guidelines. Adherence to these policies will protect the integrity of the process of publication and the reputation of NRC as a publisher.

3. Scope

The policies outlined in this document are intended to cover all aspects of the Research Journals program.

This document begins with a description of the responsibilities of authors, editors, the Editor-in-Chief, reviewers, and the publisher. The section on publishing policy treats areas such as copyright, language of publication, the use of SI units (Système international d'unités), and advertising policy.

4. Responsibilities

Authors

1. Authors have an obligation to present an accurate account of the research performed and are responsible for complete reporting of the observations made and data collected.

2. Authors must relate their work to that of others and provide complete and accurate citations so that the readers can objectively evaluate the paper.

3. The authors should describe the safeguards used to meet both formal and informal standards of ethical conduct of research (approval of a research protocol by an institutional committee, procurement of informed consent, proper treatment of animals, and maintenance of confidentiality of personal data on patients, etc.).

4. It is the responsibility of authors to ensure that manuscripts accepted for publication are free of any kind of prejudice, especially gender and racial stereotyping.

5. Co-authors of a paper should be limited to those who have made significant scientific contributions to the work reported. All authors of a paper should be able to take public responsibility for the content. All additional contributions should be indicated in a footnote or in the Acknowledgements section.

6. Authors should avoid fragmentation of research reports or submission of trivial reports, as this consumes excessive journal space and burdens the review process unnecessarily.

7. The corresponding author must give assurance that all co-authors have read and approved the manuscript as submitted. When dealing with manuscripts with more than one author, the Editor assumes that the corresponding author is responsible on behalf of the group.

8. The authors are responsible for obtaining any formal or informal approval or clearance of the paper from their institution or company before it is forwarded to Research Journals.

9. Authors must identify the sources of all information quoted and material obtained privately.

10. When a manuscript contains material (tables, figures, charts, etc.) that is protected by copyright, it is the obligation of the author to secure written permission from the holder of the copyright. Letters of permission must be sent to the Editorial Office before final acceptance of the manuscript.

11. The authors are responsible for disclosing any information that may affect the acceptance or rejection of the paper. This includes indicating if the work has been previously presented in any format (conference proceedings, abstract publication, etc.) and submitting a list of related manuscripts that the author has in press or under consideration by another journal. The paper will be considered for publication only with the understanding that it has not already been submitted to, accepted by, or published in another journal.

Editors

1. The Editor(s) is(are) responsible for the scientific calibre of the contents of their journal.

2. The Editor appoints an editorial board for the journal, subject to review by the Editor-in-Chief. The form and functioning of this board is at the discretion of the Editor, but it is usually composed of Associate Editors, who assist the Editor in assessing articles submitted for publication and act as an advisory group for the Editor as required.

3. Editors are appointed for a fixed renewable term by the Editor-in-Chief, normally 5 years.

4. The Editor may appoint one or more Assistant Editors, who may assume the Editor's responsibilities during an absence. If this absence is expected to be prolonged, an Editor pro tem may be appointed by the Editor-in-Chief.

5. It is the responsibility of the Editor to ensure that manuscripts accepted for publication meet the guidelines established for authors.

6. The Editor is responsible for ensuring that proper review procedures are followed and for making the final decision on acceptance or rejection of a manuscript. The Editor may delegate some duties to Assistant or Associate Editors, or to a temporary Editor appointed to oversee a special issue or section, but the final responsibility remains with the Editor.

7. The peer review process is carried out under the direction of the Editor. When a manuscript is deemed appropriate for consideration for publication, arrangements are made for it to be reviewed by at least two referees.

8. Referees are advisory to the Editor and do not make decisions on acceptance or rejection of a manuscript. The name of a referee will only be conveyed to an author with the explicit consent of the referee.

9. The Editor must ensure that submitted papers are dealt with in a timely manner. The Editor will endeavour to notify all authors of the receipt of the manuscript. The Editorial Office will ensure that the corresponding author is notified of any changes in status of the manuscript and all decisions that follow.

10. The Editor is responsible for ensuring that the contents of an author's paper are not divulged to anyone other than persons necessarily involved in reading the paper in the Editorial Office or reviewing it for the Editor or persons assisting in these functions.

11. The Editor should give unbiased consideration to all manuscripts and should declare any potential conflict of interest, in which case

the Editor or Editor-in-Chief should delegate the consideration of the manuscript to another Editor or to a member of the Editorial Board.

12. All files regarding an individual manuscript are the property of the Editorial Office and are to be retained by the Editor or disposed of in consultation with the Editor-in-Chief.

13. When notified of errors in facts or conclusions in a paper subsequent to its publication, the Editor, after notifying the corresponding author, is responsible for initiating publication of an erratum or a report pointing out the changes.

14. If the Editor receives convincing evidence of plagiarism, duplicate publication, or falsification of data, the Editor must initiate publication of a retraction. The Editor must notify the Editor-in-Chief as soon as possible of any serious breaches of ethical behaviour.

Referees

1. Referees are advisors to the Editor and should serve only in their areas of expertise. A referee who feels inadequately qualified to evaluate a manuscript should return it promptly to the Editor.

2. A referee who cannot give an unbiased opinion about a manuscript should declare this bias or conflict of interest to the Editor and return the manuscript promptly.

3. Referees must treat the paper as a confidential communication. If a referee wishes to seek expert advice from an associate, he/she should consult the appropriate Editor or Associate Editor before proceeding. The associate must also honour the confidentiality of the document.

4. A referee who is unable to complete the review of a manuscript in an appropriate time frame should return it to the Editor promptly.

5. All statements made by the referee must be adequately supported so that the Editor may make a well-informed decision regarding the manuscript.

6. The referee should call to the attention of the Editor any failure by an author to cite relevant work by other scientists.

7. Unpublished information, arguments, or interpretations disclosed in a submitted manuscript should not be used for the referee's own research except with the consent of the author.

Editor-in-Chief

1. The Editor-in-Chief has overall responsibility for the scientific and editorial integrity of the journals and monographs published by the NRC Research Journals program.

2. Questions regarding the scientific quality and competitiveness of the publications, as well as ethical questions (e.g., reporting of fraudulent data, duplicate publication, submission of inappropriate material), may be referred to the Editor-in-Chief.

3. The Editor-in-Chief is responsible for selecting Editors for the journals and an Editorial Board for the monograph program. The Editor-in-Chief consults broadly and may seek advice from other Editors, from the relevant scientific and engineering societies, and from relevant Editorial Boards regarding selection of a new Editor.

4. In cases where Editors are not fulfilling their obligations as outlined in this policy, the Editor-in-Chief has the authority to terminate appointments.

5. The Editor-in-Chief has the right of access to all files maintained by the Editors of NRC Research Journals' publications. The Editor-in-Chief may exercise this right when necessary to ensure that the policies and procedures of the Editorial Offices conform to the requirements outlined in this Publication Policy.

Publisher

1. The Publisher, represented by the Director of NRC's Research Journals program, is responsible for setting policies, procedures, and guidelines and for production of the journals through the Publishing Office.

2. The Publishing Office must ensure that confidentiality of the manuscripts is maintained at all stages of the pre-publishing process. Information must not be given to persons unauthorized by the author (reporters for the news media or employees of investment firms, for example) prior to the appearance of the paper in print.

3. After a manuscript has been accepted for publication, the Editor or copy editor may make redactorial changes as required but must not make substantive changes in the content of a paper without consultation with the author and the Editor.

4. The staff of the Publishing Office must alert the Editor or Editor-in-Chief concerning any substantive changes requested by an author after acceptance of the manuscript, including changes in authorship or deletion or insertion of substantial amounts of material.

5. The Publisher accepts no responsibility for statements or opinions expressed by a contributor, and a statement to this effect will appear in all publications.

5. Publishing Policy

Copyright

Once an author's paper is accepted for publication, the author transfers copyright to the National Research Council of Canada. As the holder of copyright on all original material published in the Research Journals, NRC exercises the right to grant permission to copy or republish articles or portions thereof, provided that the source of such material is fully acknowledged.

NRC reserves the right to charge for all forms of copying or publishing, such as copying for general distribution, for advertising or promotional purposes, for creating new collective works, or for resale.

Publishing in Both Official Languages

The Research Journals program of the National Research Council of Canada follows the guidelines on publishing in both official languages as outlined by the Treasury Board of Canada Secretariat (see Circular No. 1982-58, section 10). Briefly, an article is published in English or French according to the author's choice, preceded by an informative summary or abstract in both English and French.

Standard Units

In the Research Journals, metric units are used or the metric equivalents given, and the use of SI units is encouraged, as outlined in the *Canadian Metric Practice Guide* (CAN/CSA - Z234.1-89).

Advertising in Research Journals

Advertising is accepted subject to approval by the Operations Manager. All advertising must be consistent with the editorial policy and no advertisement that is detrimental to NRC or Research Journals will be accepted. The following types of advertising are accepted:

(i) Advertisements submitted by other scholarly journals may be accepted free of charge where benefit is expected for NRC publications in exchange.

(ii) Advertisements announcing upcoming conferences and symposia may be accepted free of charge, subject to approval by the Editor of the publication concerned. Such advertisements will only be accepted when the event is of interest to a significant proportion of the Canadian scientific community served by that publication. The event need not take place in Canada.

(iii) Paid advertisements may be accepted providing they are consistent with the editorial policy of the publication. No advertising that implies endorsement of a product or service by the publication, the Editorial Board, or NRC will be accepted. Loose inserts are considered to be paid advertisements.

List rental

NRC Research Journals makes available, for rental on a one-time-use basis only, the lists of subscribers to the journals. No subscriber is included on such a list when that subscriber or society has requested non-inclusion.

Government policy

All copy and visual material will conform to Treasury Board guidelines for the elimination of sexual and racial stereotyping. These are enunciated in the Treasury Board Administrative Policy Manual, Chapter 484, and Treasury Board Circular No. 1982-50, *Elimination of Sexual Stereotyping,* and No. 1984-4,*Guidelines for the Representative Depiction of Visible and Ethnic Minorities and Aboriginal Peoples in Government Communications.*

REVUES SCIENTIFIQUES POLITIQUE DE PUBLICATION[1]

1. Mandat

La Loi sur le Conseil national de recherches confère au Conseil national de recherches du Canada (CNRC) le droit de publier des documents scientifiques et techniques.

Le programme des Revues scientifiques du CNRC a pour objectif de publier, au moment opportun et de façon rentable, des revues et des monographies scientifiques et techniques de haute qualité. Les monographies et les revues scientifiques publiées par le CNRC permettent aux scientifiques et aux ingénieurs canadiens et du monde entier d'établir des liens avec leurs collègues de la communauté scientifique internationale. Les Revues scientifiques et leurs directeurs scientifiques ont pour mandat de produire des publications internationales de haute qualité, ajoutant ainsi une contribution du Canada à l'enrichissement de la documentation scientifique mondiale.

2. Raison d'être

Depuis que le CNRC a entrepris la publication de revues scientifiques en 1929, de nombreuses méthodes et procédures éditoriales ont été élaborées en suivant les usages propres à chacune des diverses disciplines. Il est important que le CNRC mette en oeuvre les méthodes déjà éprouvées dans ce domaine et, lorsque cela est possible, améliore ces méthodes. Le présent document récapitule et officialise les principes directeurs qui régissent l'édition et la production des documents scientifiques et définit une série de règles de conduite en matière de publication. La conformité à ces principes directeurs aura pour effet de protéger l'intégrité du processus de publication et la réputation du CNRC à titre d'éditeur.

3. Portée

Les principes directeurs contenus dans le présent document s'appliquent à tous les aspects du programme des Revues scientifiques.

On y trouve la description des responsabilités des auteurs, des directeurs scientifiques, du directeur général des Revues scientifiques, des examinateurs et de l'éditeur. Les questions du droit d'auteur, de la langue de publication, de l'emploi du Système international d'unités (SI) et des règles en matière de publicité font l'objet de la section Politique de publication.

4. Responsabilités

Auteurs

1. L'auteur d'un article a l'obligation de fournir un compte rendu exact des travaux de recherche exécutés et de rapporter de façon complète les observations effectuées et les données recueillies.

2. L'auteur doit mettre ses travaux en rapport avec ceux d'autres chercheurs et fournir des références complètes et exactes de façon à ce que le lecteur puisse évaluer l'article d'une manière objective.

3. L'auteur doit décrire les mesures qui ont été prises dans le but de satisfaire aux normes formelles et informelles de l'éthique régissant la recherche (autorisation d'un protocole de recherche par un comité de l'établissement, obtention d'un consentement éclairé, traitement approprié des animaux et confidentialité des données personnelles sur les malades, etc.).

4. Il appartient à l'auteur de s'assurer que le langage utilisé dans son article ne soit pas entaché de préjugés, et en particulier que l'article ne contienne pas de stéréotypes sexuels ou raciaux.

5. Seule une personne ayant contribué de façon importante du point de vue scientifique aux travaux rapportés peut être désignée coauteur d'un article. Tous les auteurs d'un article doivent être en mesure d'assumer la responsabilité publique du contenu de cet article. Toutes les autres contributions peuvent être signalées dans une note infrapaginale ou dans la section Remerciements.

6. L'auteur devrait s'abstenir de fragmenter un rapport de recherche et de soumettre des rapports ne présentant aucun intérêt particulier afin de ne pas réduire indûment l'espace de publication disponible et alourdir inutilement le processus d'évaluation.

7. L'auteur correspondant doit donner l'assurance que tous les coauteurs ont lu et approuvé le manuscrit tel qu'il a été soumis. Lorsqu'un manuscrit comporte les noms de plusieurs auteurs, le directeur scientifique tient pour acquis que l'auteur qui soumet l'article est responsable pour le groupe.

8. Il appartient à l'auteur d'obtenir auprès de son établissement ou de son entreprise tout consentement ou autorisation nécessaire avant de soumettre un article aux Revues scientifiques.

9. L'auteur a l'obligation d'indiquer la source de toute information citée et de tous documents dont il a obtenu copie à titre personnel.

10. Lorsqu'un manuscrit renferme des données (tableaux, figures, schémas, etc.) protégées par le droit d'auteur, il appartient à l'auteur de l'article d'obtenir la permission écrite du détenteur du droit d'auteur. Les lettres d'autorisation doivent parvenir au Bureau de la rédaction avant l'étape de l'approbation finale du manuscrit.

11. L'auteur est tenu de divulguer tout renseignement pouvant avoir une incidence sur la décision d'accepter ou de refuser l'article. Il doit donc indiquer si les travaux rapportés ont déjà fait l'objet d'une quelconque présentation (comptes rendus de conférence, résumés, etc.) et fournir la liste des articles associés à ces travaux et sur le point d'être publiés ou qui ont été soumis à une autre revue scientifique. L'article ne sera évalué aux fins de publication qu'à la condition de n'avoir pas déjà été proposé à une autre revue, accepté pour publication ou publié par une autre revue scientifique.

Directeurs scientifiques

1. Le(s) directeur(s) scientifique(s) est (sont) responsable(s) du maintien du caractère scientifique du contenu de la revue dont il(s) a (ont) la charge.

2. Les membres du comité de rédaction d'une revue sont nommés par le directeur scientifique avec l'approbation du directeur général. La structure et le fonctionnement du comité sont généralement laissés à la discrétion du directeur scientifique; toutefois, un comité de rédaction est habituellement composé de directeurs scientifiques associés dont la tâche consiste à prêter main-forte au directeur scientifique concernant l'évaluation des articles soumis pour publication et à le conseiller si besoin est.

3. Les directeurs scientifiques sont nommés par le directeur général pour des mandats renouvelables fixes, d'une durée habituelle de 5 ans.

4. Le directeur scientifique a le loisir de nommer un ou plusieurs directeurs scientifiques adjoints qui peuvent assumer ses fonctions en son absence. S'il est prévu que cette absence se prolongera, le directeur général pourra nommer un directeur provisoire.

5. Il appartient au directeur scientifique de s'assurer que tous les manuscrits acceptés respectent les directives à l'intention des auteurs.

6. Il revient au directeur scientifique de veiller à ce que les manuscrits soient évalués selon les règles et de prendre la décision finale quant à l'acceptation ou au rejet d'un manuscrit. Le directeur scientifique peut déléguer certaines de ses tâches aux directeurs scientifiques adjoints ou associés ou à un directeur scientifique provisoire nommé pour coordonner la publication d'un numéro spécial ou d'une rubrique particulière; en dernière analyse, le directeur scientifique demeure toutefois le seul responsable de la Revue.

7. Le directeur scientifique dirige le processus d'évaluation des manuscrits par les pairs. Un manuscrit qui répond aux exigences du processus d'évaluation doit être examiné par au moins deux examinateurs.

[1] Dans le présent document, à moins d'indication contraire dictée par le contexte et pour éviter d'alourdir le texte, l'emploi du masculin comprend le féminin.

8. Les examinateurs n'ont qu'un pouvoir consultatif auprès du directeur scientifique et ne prennent aucune décision quant à l'acceptation ou au refus d'un manuscrit. Le nom d'un examinateur ne peut être communiqué à l'auteur d'un article qu'avec le consentement explicite de cet examinateur.

9. Le directeur scientifique doit veiller à ce que les articles soumis soient traités dans des délais opportuns. Il s'efforcera de faire parvenir un accusé de réception du manuscrit à tous les auteurs. Le Bureau de la rédaction veillera à informer l'auteur correspondant de tout changement de statut du manuscrit et de toutes décisions subséquentes.

10. Le directeur scientifique doit s'assurer que le contenu d'un article n'est pas communiqué à des personnes autres que celles nécessairement mises à contribution à l'étape de la lecture du manuscrit au Bureau de la rédaction, et à celle de l'évaluation par le directeur scientifique ou les personnes qui l'assistent.

11. Le directeur scientifique doit examiner les manuscrits en toute impartialité. Il doit déclarer tout conflit d'intérêts possible. Dans un tel cas, le directeur scientifique ou le directeur général remettra le manuscrit à un autre directeur scientifique ou à un membre du Comité de rédaction.

12. Tous les dossiers associés à un manuscrit sont la propriété du Bureau de la rédaction et sont conservés par le directeur scientifique. Ce dernier peut aussi s'en départir, sous réserve de l'approbation du directeur général.

13. Il incombe au directeur scientifique d'informer l'auteur des erreurs dans les faits ou les conclusions qui pourraient lui être rapportées après la publication d'un article et de prendre les dispositions nécessaires afin de publier un erratum ou un rapport indiquant les changements.

14. S'il obtient des preuves convaincantes qu'il y a eu plagiat, publication en duplicata ou falsification de données, le directeur scientifique doit prendre les dispositions nécessaires pour publier des rétractations. Il doit informé le directeur général de tout manquement sérieux à l'éthique.

Examinateurs

1. Les examinateurs n'ont qu'un rôle consultatif auprès du directeur scientifique et ne devront opérer que dans leur domaine de compétence. Un examinateur qui s'estime insuffisamment qualifié pour évaluer un manuscrit devra le retourner promptement au directeur scientifique.

2. Un examinateur qui n'est pas en mesure de donner une opinion impartiale sur un manuscrit devra en aviser le directeur scientifique ou l'aviser de l'existence d'un conflit d'intérêts et retourner le manuscrit sans délai.

3. Les examinateurs doivent traiter les articles en toute confidentialité. Si un examinateur désire obtenir l'opinion experte d'un collègue, il devra consulter le directeur scientifique ou le directeur scientifique associé avant de poursuivre son travail. Ledit collègue devra également respecter le caractère confidentiel du document.

4. Un examinateur qui se trouve dans l'impossibilité d'achever l'évaluation d'un manuscrit dans les délais prescrits devra le retourner promptement au directeur scientifique.

5. Les avis donnés par l'examinateur devront s'appuyer sur une argumentation solide qui permette au directeur scientifique de prendre la décision qui s'impose en ce qui concerne le manuscrit.

6. L'examinateur devra porter à l'attention du directeur scientifique toute omission de la part d'un auteur de citer des travaux pertinents d'autres scientifiques.

7. L'information et les argumentations non encore publiées, ou les interprétations divulguées dans un manuscrit déjà soumis, ne devront pas être utilisées pour les propres travaux de recherche de l'examinateur sans l'autorisation de l'auteur.

Directeur général des Revues scientifiques

1. Le directeur général a la responsabiiité globale de l'intégrité scientifique et éditoriale des revues et monographies publiées dans le cadre du programme des Revues scientifiques du CNRC.

2. Les questions relatives à la qualité et à la compétitivité scientifiques des publications ainsi que les questions d'éthique (données frauduleuses, publication en duplicata, remise de documents inappropriés) peuvent être soumises au directeur général.

3. Le directeur général est chargé de la sélection des directeurs scientifiques des revues et d'un comité de rédaction pour le programme de monographies. Le directeur général recueille le maximum d'avis et peut solliciter ceux d'autres directeurs scientifiques, de sociétés scientifiques et d'ingénierie, et de comités de rédaction compétents pour le recrutement d'un nouveau directeur scientifique.

4. Dans les cas où les directeurs scientifiques ne remplissent pas leurs obligations en ce qui concerne les critères énoncés dans la présente politique, le directeur général a le pouvoir d'exiger leur démission.

5. Le directeur général a droit d'accès à tous les dossiers administrés par les directeurs scientifiques des publications des Revues scientifiques du CNRC. Le directeur général peut exercer ce droit lorsque nécessaire pour s'assurer que les politiques et procédures des bureaux de la rédaction sont conformes aux dispositions énoncées dans la Politique de publication.

Éditeur

1. L'éditeur, représenté par le directeur du programme des Revues scientifiques du CNRC, est chargé de l'établissement de politiques, de procédures et des directives ainsi que de la production des revues scientifiques par l'intermédiaire du Bureau des publications.

2. Le Bureau des publications doit s'assurer que la confidentialité des manuscrits est maintenue à toute les étapes du processus qui précède la publication. L'information ne peut être communiquée à qui que ce soit (représentants des médias ou employés de maisons d'investissement, par exemple) sans l'autorisation de l'auteur avant la publication.

3. Après acceptation du manuscrit pour publication, le directeur scientifique ou le rédacteur technique pourra éventuellement effectuer des modifications rédactionnelles mais il ne devra pas modifier substantiellement le contenu d'un article sans consulter l'auteur ou le directeur scientifique.

4. Le personnel du Bureau des publications doit aviser le directeur scientifique ou le directeur général de tout changement substantiel demandé par un auteur après acceptation du manuscrit, ceci incluant les changements de noms d'auteurs ainsi que les suppressions ou les insertions atteignant un volume substantiel.

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Risk Evaluation and Biological Reference Points for Fisheries Management

Dans la publication spéciale des sciences halieutiques et aquatiques n° 120

Du 19 au 22 novembre 1991, le Comité Scientifique Consultatif des Pêches Canadiennes dans l'Atlantique (CSCPCA), ministère des Pêches et des Océans, a tenus à Halifax, Nouvelle-Écosse, un atelier intitulé « Évaluation des risques et points de référence biologiques en gestion des pêches ». Soixante chercheurs et économistes du domaine des pêches, en provenance d'Australie, du Canada, de la Finlande, de la France, de l'Islande, de la Nouvelle Zélande, de la Norvège, de l'Afrique du Sud, du Royaume-Uni et des États-Unis, y ont participé. Ce doucument renferme 31 articles présentés au cours de trois sessions thématiques. La première session a servi à faire le point sur l'utilisation, la performance, les forces et les faiblesses des points de référence biologiques d'usage général (e.g., F_{med}, $F_{0.1}$, BSR/R). Les articles présentés au cours de la deuxième session ont touché au méthodes d'identification et d'estimation des incertitudes associées à l'utilisation de divers points de référence. Les stratégies de gestions fondées sur de nouveaux points de référence ainsi que des suggeestions pour faire face à de nouvelles situations (e.g., développement de nouvelles ressources halieutiques, gestion de complexes de stocks) ont fait l'objet de la trosième session. Ce doucument contient également le rapport des quatre groupes formés afin d'adresser des questions spécifiques sur l'application de l'évaluation des risques et de points de références biologiques. Les résponses apportées ont étés présentés par chaque groupe en session plénière à la fin de l'atelier. Tous les groupes ont soulevé que, bien qu'il en est de la responsabilité des chercheurs d'évaluer les différentes stratégies de gestion, l'établissement des objectifs à rencontrer au moyen de ces stratégies doit être fait par les gestionnaires.

DIRECTEURS SCIENTIFIQUES
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Risk Evaluation and Biological Reference Points for Fisheries Management

In the Canadian Special Publication of Fisheries and Aquatic Sciences No. 120

The Canadian Atlantic Fisheries Scientific Advisory Committee (CAFSAC) of the Canadian Department of Fisheries and Oceans sponsored a workshop on Risk Evaluation and Biological Reference Points for Fisheries Management, November 19-22, 1991, in Halifax, Nova Scotia. This meeting was attended by 60 fisheries scientists and economists from Australia, Canada, Finland, Iceland, New Zealand, Norway, South Africa, the United Kingdom, and the United States. This volume contains 31 papers presented at the workshop in three theme sessions. In the first session, the use, track record, strengths and weaknesses of commonly used biological reference points (e.g., F_{med}, $F_{0.1}$, SSB/R) were reviewed. Papers in the second session were focussed on methods for identifying and quantifying the uncertainties associated with using various reference points. Alternative management strategies based on new reference points or suggested strategies for dealing with novel situations (e.g., developing new fisheries resources, management of stock complexes) were the subject of the third session. This volume also includes the reports of four working groups formed to answer specific questions on the application of risk evaluation and biological reference points. These answers were presented by each group in plenary session at the end of the meeting. One common thread which ran through all the working group presentations was the emphasis on the scientists' responsibility to evaluate the different management strategies and the managers' responsibility to establish the objectives to be met by these strategies.

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